The ecology of the alder aphid "Pterocallis alni" (Degeer) and its role in integrated orchard pest management

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The Ecology of the Alder Aphid (*Pterocallis alni* (Degeer)) and its role in Integrated Orchard Pest Management

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To my Mother and Father

and Janet

ABSTRACT

The black-kneed capsid bug, Blepharidopterus angulatus (Fallen) is an important colonizer of orchards in late summer. Capsids develop on alder windbreaks feeding on the aphid Pterocallis alni (Degeer). When the aphid population declines adult bugs move to nearby orchards where they feed on pest species. The biology and ecology of P.alni has been examined in order that predator populations may be manipulated.

Aphid populations increase rapidly to a peak, then suddenly decline. A high initial population results in a peak in mid July, low initial numbers result in a peak in early August. Pruning of the windbreaks can alter the population cycles of the aphid.

P.alni is polymorphic and crowding results in the production of winged individuals. The crowding stimulus acts pre and post natally. Flight is stimulated by crowding and emigrating alatae colonize other alder trees.

Sexual forms of the aphid are produced as a response to a shortening of the daylength in autumn. In field conditions adult aphids produce a reproductive sequence of virginoparae, males and finally oviparae. Egg laying and distribution were examined and winter mortality monitored. Arthropod predators are the main cause of egg loss and greatest mortality occurs in early winter.

The food quality of alder leaves for the aphids deteriorates in early summer. Poorer food, rising temperatures and increased crowding result in smaller aphids which are less fecund. Recruitment to the population falls and numbers collapse when emigration exceeds recruitment.

The emigration of B.angulatus from alder is closely synchronized with the abundance of P.alni. The key mortality factor in bug populations is the

loss of reproductive females. However, female capsids tend to remain on the windbreak unless their prey disappears completely. If this occurs, both sexes will migrate to the orchard.

Capsid numbers and movements are indirectly affected by cultural practices of the alder resulting in changes in aphid abundance.

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Chapter 1. INTRODUCTION

Pest control procedures fall naturally under a number of headings such as chemical control, biological control and cultural control. These are descriptive of the techniques involved and were for some time distinct well-defined categories. Some relatively recent procedures cut across these established boundaries and there is now a strong tendency to use two or more approaches together in systems of integrated control or pest management.

Many definitions of pest management have been proposed but perhaps the most suitable is that of Brader (1979) who stated that "pest management is a system that, in the context of the associated environment and the population dynamics of the pest species, utilises all suitable techniques and methods in as compatible a manner as possible and maintains pest populations at levels below those causing economic injury".

Recent trends in orchard pest control have involved the integration of biological, chemical and cultural control with emphasis placed on the need to be aware of pest, predator and parasite population changes and to maximise the contribution of predators and parasites by the use of selective chemicals applied when pest species exceed threshold levels (Hoyt and Burts,1974; Skinner, 1983).

At present most orchard pests are controlled reasonably easily by the available range of insecticides (A.L.Winfield, pers.comm.). Problems have arisen in the past with the development of resistance to various chemicals by one of the most important pests of all, the fruit tree red spider mite, Panonychus ulmi (Koch) (Cranham, 1982 a,b). There is now a suggestion that the apple rust mite, Aculus schlectendali (Nalepa) is developing resistance and the pear sucker, Psylla pyricola Förster also has developed resistance in south-east England. This latter insect may now be controlled by chemical

applications and the action of natural enemies such as anthocorid bugs (Campbell, Easterbrook and Souter, 1984). New chemicals are costly to develop and therefore methods of integrated control will be needed to relieve the selection pressure for resistance in insects and mites regularly controlled by chemicals.

The modern orchard is very different from those planted in the past. Trees tend to be smaller, for ease of harvesting and chemical application. Herbicides are applied to the ground flora to reduce competition for water and nutrients and elimimate secondary hosts for pests, such as plantains for the rosy apple aphid Dysaphis plantaginea (Passerini). Windbreaks are now a common feature and belts consisting of alder species have been planted extensively over the last fifteen years (Solomon, 1981). Lewis and Smith, (1969) showed that a 7m tall netting windbreak afforded a considerable degree of shelter and insects of many species were three times as abundant in a sheltered orchard. The presence of a windbreak can give increased and earlier crop yields, provide shelter for pollinating insects, reduce soil erosion and reduce the risk of wind-borne diseases such as mildews or rusts (Baxter, 1979). The main reason for planting and maintaining a windbreak is to filter the wind and reduce its speed. Pesticide application is then easier in sheltered conditions. Windbreaks can also be sources of orchard pests and predators (Solomon, 1981) and care has been taken in the past to ensure that planting a windbreak does not simply provide an alternative habitat for fruit pests.

Alders have been extensively used as windbreaks because they grow moderately tall, are easily managed by pruning, fix nitrogen and thrive on a range of soils (Baxter, 1979). They have very few phytophagous arthropods in common with fruit trees (Solomon, 1981) and therefore pose no threat to pest management in orchards. Species which have been planted are the Common Black Alder, Alnus glutinosa (L.) Gaertner, a species native to Britain and

two introduced species, Alnus incana (L.) Moench or Grey Alder from northern Europe and Alnus cordata Desfontaines or Italian Alder from southern Europe. Solomon (1975 a,b) reported that alder windbreaks provided a habitat for the development of the black-kneed capsid bug, Blepharidopterus angulatus (Fallen). This predatory mirid, the biology of which was studied by Collyer (1952) was shown to colonize orchards in late summer apparently by migration from alder windbreaks. Solomon (1981) reported that with the planting of alder windbreaks, a considerable reservoir of B.angulatus had been established close to many orchards and that this bug had potential in an integrated control system for pests such as P.ulmi whose numbers it can prevent from becoming abundant in unsprayed orchards (Collyer, 1953). In this respect alder may be a source of beneficial natural enemies, similar to stinging nettles where coccinellidae may develop on the aphids there (Perrin, 1974) or Ash, where the reservoir may be of insect parasitoids (Stary, 1982).

Solomon (1975b) considered that B.angulatus when developing on alder fed on aphids and leafhoppers. Skinner (1983) in a review of apple aphids and their predators suggested that the possible prey were psyllids, leafhoppers and the aphid Pterocallis alni (Degeer). At the time when the capsid nymphs were present the only prey of a suitable size and in sufficient quantities was P.alni. Skinner (1983) also stated that B.angulatus colonizes orchards in late summer where it feeds on apple aphids in addition to mites. This study attempts to quantify movement of the predator, elucidate the reasons for its migration and examine how this may be managed.

The changes in abundance of predators reflect changes in abundance of their prey. The study of the dynamics of competition and predation (e.g.Hassell, 1976) can be complex. In order to manipulate numbers of B.angulatus so that the bugs may be reliable in appearance and be produced in numbers likely to exert control over orchard pests we need to know the dynamics of its prey

populations in detail. By understanding the factors influencing changes in abundance of P.alni we may examine how these affect capsid abundance and how such changes may be manipulated to establish B.angulatus as a useful component of a successful integrated pest control system.

P.alni is a member of the aphid family Callaphididae. It is a small pale green aphid, viviparous forms of which may be apterous or alate. It is not ant-attended and lives under leaves of A.glutinosa (Stroyan, 1977). It is holocyclic, producing sexual forms in autumn. Overwintering occurs as eggs, these being laid in crevices in the bark of its host plant. Eggs are covered with powdery wax, secreted from large wax gland fields situated ventrolaterally below the siphunculi and applied during oviposition. Eggs hatch in spring producing fundatrices which are apterous. These give rise to generations which may be apterous (plate 1) or alate (plate 1). Both forms can occur within one generation. With the onset of autumn winged males and apterous oviparae appear and eggs are again produced.

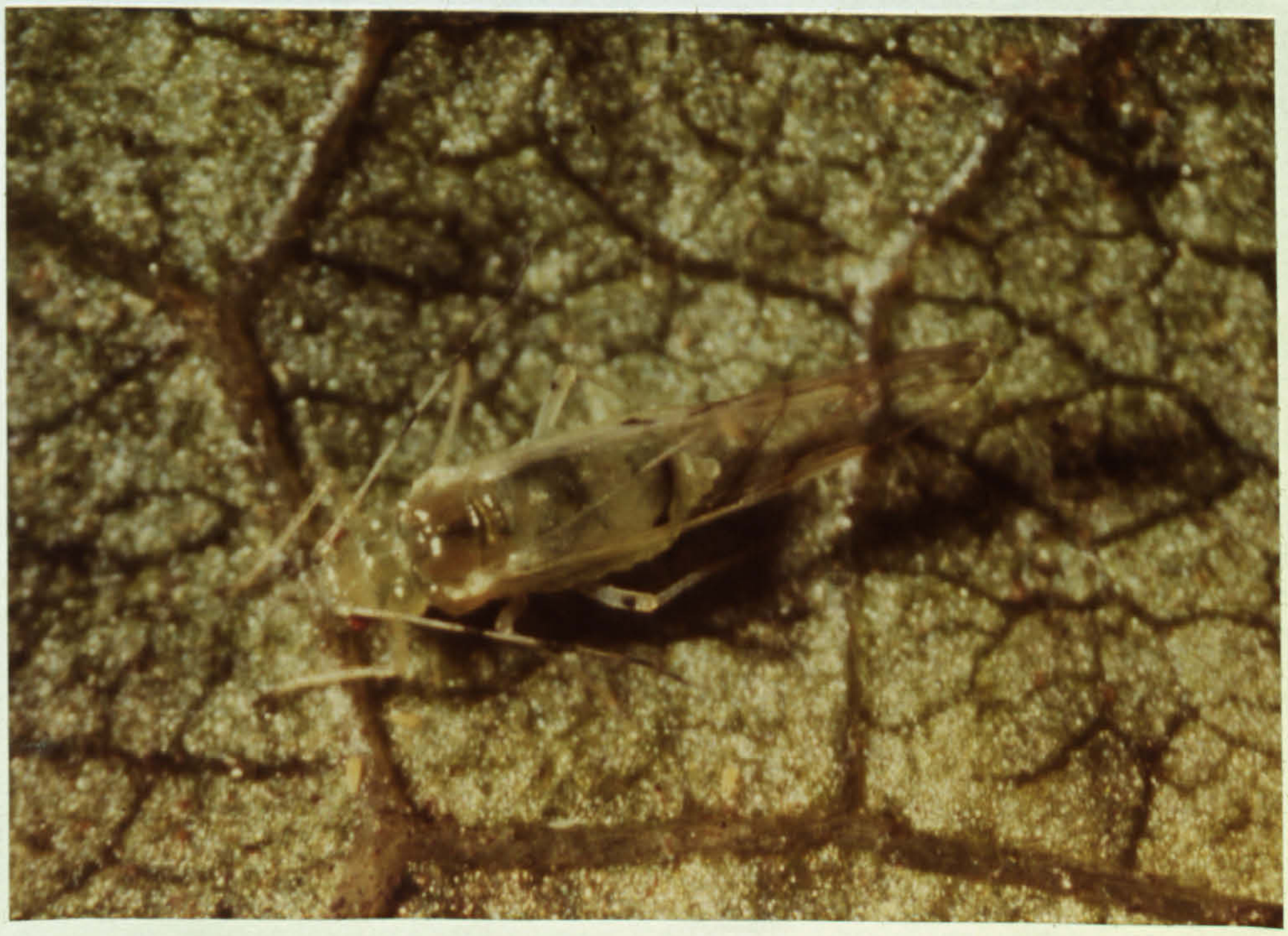
The ecology of aphids has been comprehensively reviewed by Dixon (1985a). In this respect 'ecology' is used as a broad term to include aspects of the basic biology of aphids, necessary in an understanding of their population changes. In this study the ecology of P.alni is examined through the analysis of population studies and laboratory investigations of its biology. Populations are studied in a frequently changing habitat on alder windbreaks and in a more constant situation where pruning and spray drift do not occur. This is the first reported population study of an arboreal callaphid which exhibits alary polymorphism. The factors affecting wing production and those concerning the production of sexual forms are investigated and related to changes in abundance observed in the field. The growth and reproduction is described in the field and under controlled laboratory conditions and changes in abundance as a result of these factors discussed.

PLATE 1

Adult virginoparae of P.alni

(a) Aptera and young nymph

(b) Alata



The interactions between B.angulatus and P.alni in field and laboratory are described and the role of both species in integrated control considered. The manner in which numbers of these may be manipulated is discussed and recommendations given for the role of windbreaks, predators and prey in a successful system of orchard pest management.

Chapter 2. THE POPULATION DYNAMICS OF P.ALNI

2.1. INTRODUCTION

2.1.1. Population studies of aphids

Population studies of aphids present many problems rarely met with in univoltine insects. Many aphids are highly polymorphic. The relatively short development time and long reproductive life result in overlapping generations often with unstable age distributions. Parthenogenesis, a characteristic of aphids has been of great importance in determining the structure of aphid populations (Dixon, 1985b). It led to the evolution of polymorphism and the associated division of roles within clones. It also led to the telescoping of generations, enabling numbers to increase at prodigious rates.

For practical and economic reasons most studies have concentrated on species which rise to pest status on single, uniform crops (van Emden, Eastop, Hughes and Way, 1969). Sharaf Eldin (1970) investigating changes in aphid numbers on potatoes found that rain and pathogenic fungi restricted the increase of Macrosiphum euphorbiae (Thomas) . Although excluding predators revealed that these influenced populations of Myzus persicae (Sulzer), the poor food quality of the potato host appeared to be the most important factor in determining population change. Trumble (1982a) also concluded that predators and parasites did not reduce M.persicae numbers on broccoli in California.

Sharaf Eldin (1970) noted that a high infestation of M.persicae on potatoes occurred when colonizing alatae arrived in large numbers. A similar situation appears to exist with mid summer populations of Aphis fabae Scopoli on field beans (Way, 1967). Subsequent numbers are self regulated by food and space available on the growing plant and limited by predation from natural enemies (Way and Banks, 1967). The colonization of cereal crops by aphids also appears to affect subsequent populations (Dean,1973; Rabbinge, Ankersmit and Pak, 1979). However, weather conditions such as

spring temperatures are thought to play a major role in the population build up of Metapolophium dirhodum (Walker) on cereals (Ankersmit and Carter, 1981).

Other population studies of aphids infesting grain crops include those of Hamilton, Kirkland and Perries (1982) and Summy and Gilstrap (1983) involving Schizaphis graminum (Rondani) on sorghum in Missouri and Texas. The first authors state that the natural enemies present (mainly coccinellids, anthocorid bugs and neuropteran larvae) were capable of regulating aphid populations under a wide range of environmental conditions. The latter authors considered the emigration of alates to be a major cause of populations declining in mid summer. Milne (1971) investigating the effects of aphid predators on field beans found that birds caused high mortality of Megoura viciae (Buckton) whereas invertebrate predators were more important for A.fabae. However, with both these species and Acyrthosiphon pisum (Harris), intraspecific competition resulting in a suppression of natality and emigration of alates was the main factor causing population changes.

Changes in the host plant have been shown to account for changes in the populations of Chaetosiphon fragaefolii (Cockerell) on strawberries by Dicker (1952) and Trumble, Oatman and Voth (1983). The latter authors concluded that density independent mortality factors, namely temperature and plant physiology were more important than natural enemies. The critical role of the host plant in population dynamics has also been shown for other monophagous aphids. Smith (1957) found that a drop in food quality and predation by birds checked and caused populations of Acyrthosiphon spartii (Koch) on broom, Sarothamnus scoparius L. to decline. Extreme examples of this are provided by Masonaphis maxima (Mason) on thimbleberry, Rubus parviflorus Nuttall (Frazer and Forbes, 1968) and Mindarus abietinus Koch on Fraser Fir trees (Nettleton and Hain, 1982). In both cases, sexuals were produced in late May and June, exceptionally early in the climates of

Vancouver and North Carolina, as a result of cessation of production of young foliage on which the aphids feed.

The cabbage aphid, Brevicoryne brassicae (L). has been studied in Europe by Hafez (1961) who concluded that mid summer declines were caused by predators. An in-depth study by Hughes (1963) in Australia revealed that complex interactions between biotic and abiotic factors determined patterns of abundance.

Less attention appears to have been paid to non-pest species on perennial hosts. The dynamics of Microlophium evansi (Theobald) on stining nettle, Urtica dioica L. was studied by Perrin (1974). It was concluded that a reduction in host plant quality and emigration of alates contributed to population decline. Sub-optimal temperatures and natural enemies affected the populations thereafter.

Much information has been gained by thorough investigations of the population dynamics of Eucallipterus tiliae (L)., the lime aphid and Drepanosiphum platanoidis (Schrank) on sycamore. Neither parasites nor predators were found to be important in regulating numbers of these aphids (Dixon,1977). Both species have been shown to induce changes in the metabolism of their hostplants (Dixon 1970a, 1971 a & b). These changes do not appear to affect numbers of E.tiliae (Dixon,1971c) but they can have a stabilizing effect on D.platanoidis populations (Dixon, 1970a). In E.tiliae the causal mechanism of population decline is intraspecific. High densities result in proportionately more migratory activity and the production of small individuals with low reproductive rates. The converse is also true. These changes result in the general population oscillating from year to year (Dixon,1971c). D.platanoidis undergoes reproductive diapause in summer due to the poor quality of its host (Dixon,1963) and this is accentuated by high aphid densities in early summer (Dixon,1966). Whilst the basic pattern of

fluctuation appears to be controlled by host plant quality, the size of the population is additionally influenced by the numbers present in spring and the history of aphid attack on the host (Dixon,1970a and b; Chambers,1979). Other tree dwelling aphids whose dynamics appear to be related to host plant quality are the birch aphid, Euceraphis punctipennis (Zetterstedt) studied by Wratten (1974), Chromaphis juglandicola (Kaltenbach) on walnut (Sluss,1967) and Tuberculoides annulatus (Hartig) on oak (Lorriman, 1980). Populations of C.juglandicola and T. annulatus were also affected by predation and emigration respectively.

From this review it may be seen that the factors influencing change in aphid populations are many and vary from species to species. The current study aims at an investigation of the population changes of P.alni within and between years. It attempts to establish which factors exert the greatest influence on the population dynamics of this aphid.

2.1.2. Special features of P.alni

As stated previously, P.alni is a monophagous tree dwelling aphid. In this respect it is similar to other members of the Callaphididae mentioned above namely E.tiliae, D.platanoidis, C.juglandicola, E.punctipennis, and T. annulatus. The viviparae of all these species are alate; however those of P.alni may be apterous or alate (Stroyan,1977). The P.alni fundatrix is always apterous and successive generations of viviparae throughout the summer contain variable proportions of apterous and alate individuals. Due to the differences in biology, P.alni may show differences in its population dynamics to the above callaphididae. It may be most similar to the dynamics shown by M.evansi (Perrin 1974) as this species also exhibits facultative alate production.

2.2. MATERIALS AND METHODS

2.2.1. Sites of study

Orchard studies were carried out at East Malling Research Station, Maidstone, Kent from March 1982 to November 1984.

Windbreaks of Alnus glutinosa were sampled in two parts of the farm. These were designated LF125 and WM110 on the farm plan. LF125 was parallel to and 60m opposite a mixed windbreak of A.cordata, A.incana and A.rubra designated LF126 (fig.1a). A fallow field separated the two windbreaks and on one side of each were planted nursery stock fruit trees. WM110 was at right angles to WM109, a pure A.cordata windbreak (fig.1b). On either side of WM110 were plum, apple and pear orchards. The windbreak is usually pruned annually in mid summer. This ensures that it does not compete with the crop, restrict light and access or take up too much productive space. In order to be able to compare the population on a windbreak which has been pruned with one which has not, certain sections were left unpruned in summer and cut the following winter.

A site at Lyne, near Virginia Water, Surrey (grid ref.TQ006674) was sampled in order to compare the natural population dynamics of P.alni with those on the managed windbreaks at East Malling. Here, young trees up to 6m high were present. The site contained A.glutinosa, A.incana and A.cordata. Another alder was found and was identified as A.hybrida A.Braun (A.Mitchell, pers.comm.). This is a natural hybrid between A.glutinosa and A.incana.

2.2.2. Sampling procedure

No one sampling method can be used for all aphids. Previous population studies have used many techniques, mainly determined by the form of the host plant. Thus, for annual crops the whole plant may be sampled and all

Figure 1:

Arrangement of windbreaks at East Malling

(a) LF 125 and LF 126

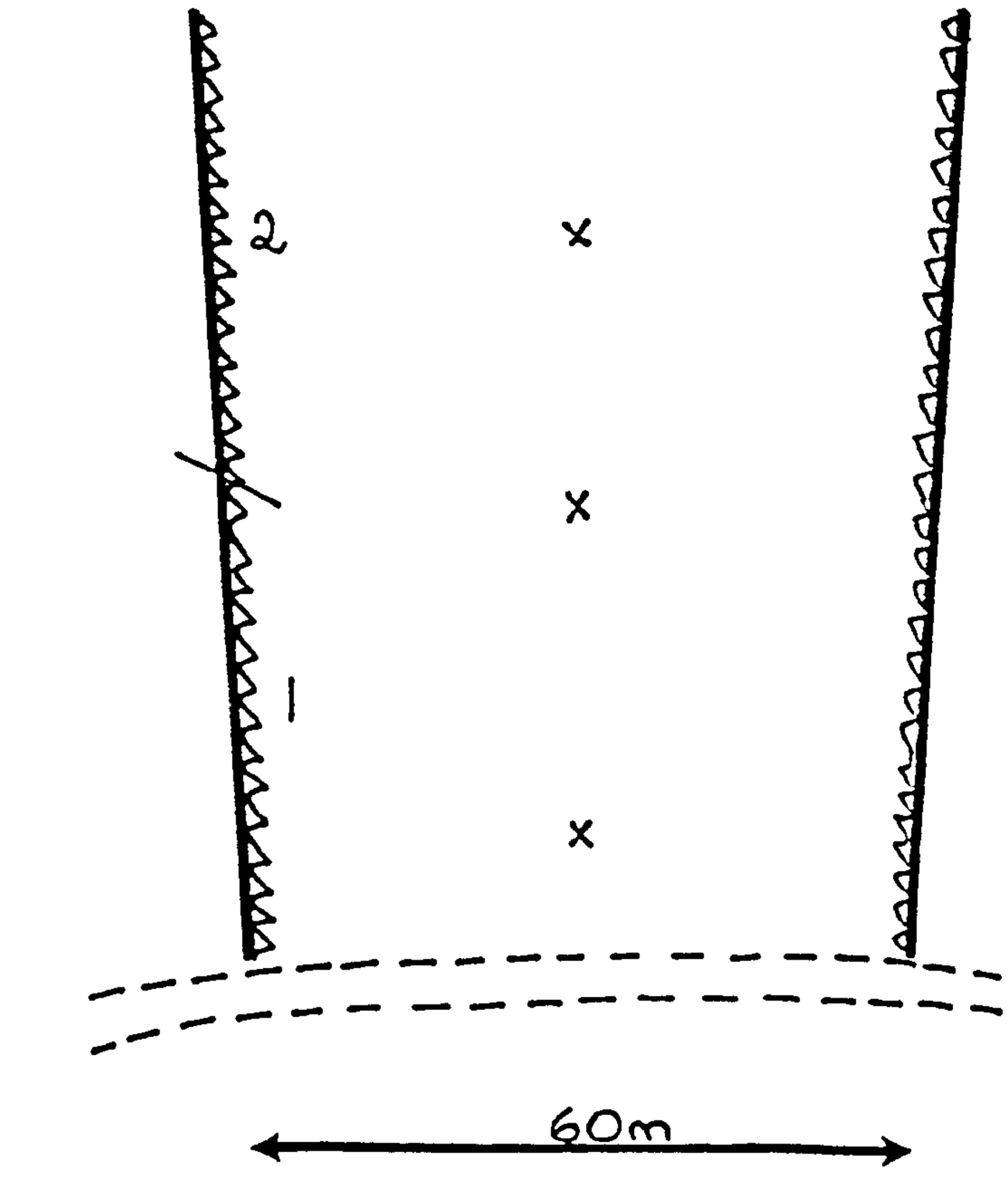
(b) WM 109 and WM 110

X position of sticky traps

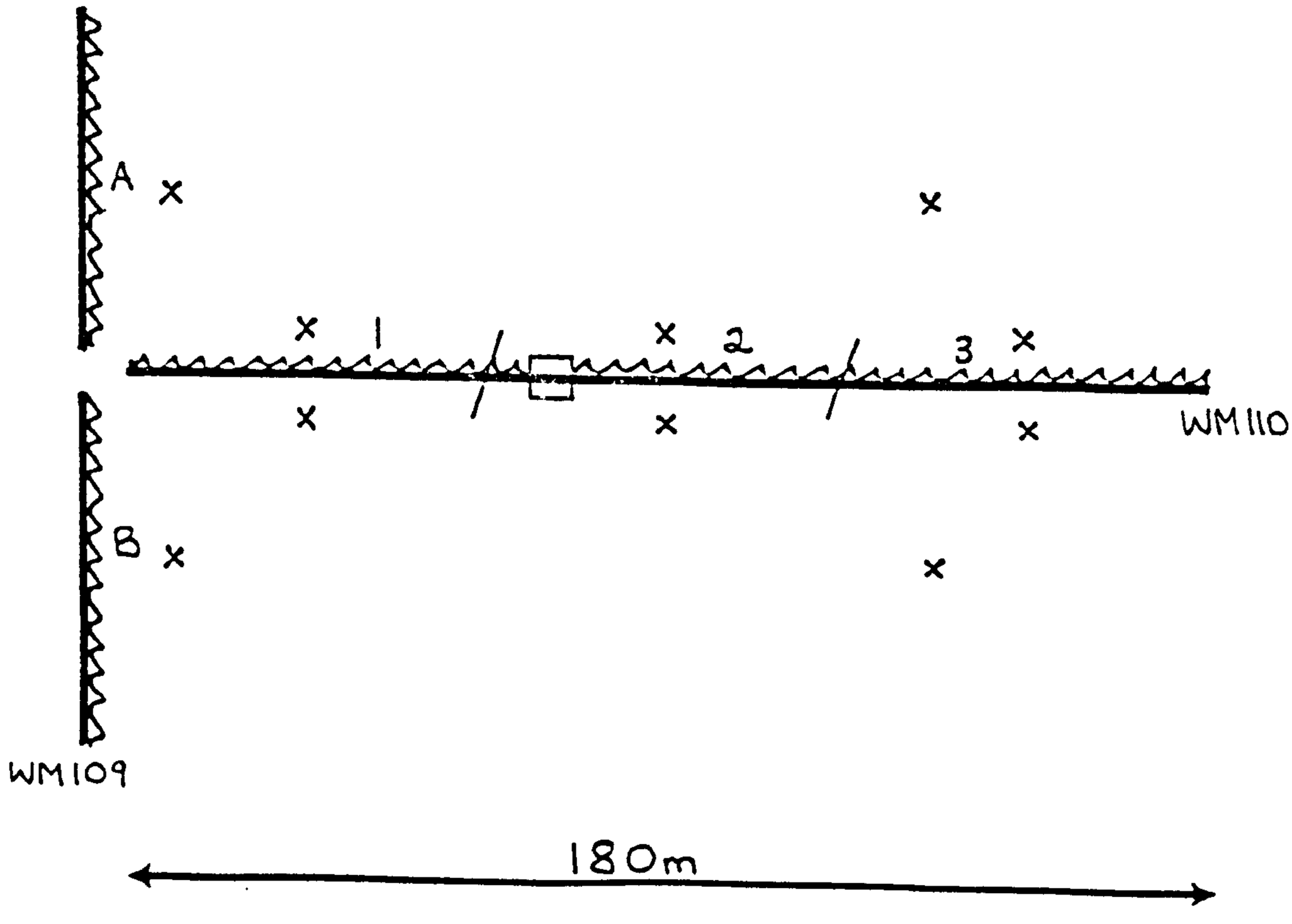
scaffold tower

sampled face of windbreak

(a)



(b)



aphids upon it counted (Hughes,1963). A destructive sampling technique was also employed by Perrin (1974) who cut 100 nettle stems for counting M.evansi numbers. Procedures such as these are obviously time consuming and leaf subsamples may be found to be as reliable (Trumble, 1982b). Sampling techniques for tree-dwelling aphids have involved selecting a number of leaves at random. Wratten (1974) divided the leaves sampled into two categories; those at the end of a twig (terminal) and those elsewhere on the branch (non-terminal). The birch twigs sampled had actively growing leaves well into mid summer and differences in aphid numbers were found. The young leaves offered favourable feeding sites, resulting in higher numbers of aphids upon them. A similar occurrence was noted with D.platanoidis on sycamore (Dixon and McKay, 1970), however the situation only existed early in the year, leaf growth being complete by mid June.

At East Malling random samples of one hundred terminal and one hundred non-terminal leaves were selected. Trees sampled were selected using a random number table. A sample of five terminal and five non-terminal leaves were randomly selected from the foliage of each tree. Thus ten leaves were sampled on each of twenty trees. Leaf samples were taken on one face of each windbreak, the other face undergoing a normal pruning regime (fig.1). The vertical distribution of aphids was also examined by the use of a scaffold tower. Random two-hundred leaf samples were taken on three trees at 3.5m (middle) and 7.5m (top) of the windbreak. The entire windbreak samples were taken between 0 - 1.5m above ground level.

Counts of aphids on each leaf were taken weekly from bud burst in early April until leaf fall in late November. The first three instars are difficult to distinguish in the field and were classified together. Fourth instars were identifiable by size and colour (potential apterae) or by the possession of wing buds (potential alatae). These were counted separately

as were viviparous adults (apterae and alatae) and sexuales (winged males and apterous oviparae). Natural enemies present upon the leaf were also counted and their life stage recorded. The number of dead aphids caused by entomopathogenic fungi and parasitism were also counted. Parasite cocoons, formed within the dead aphid's body were easily visible on the leaves being straw coloured (plate 2) and were classified as 'emerged' or 'unemerged'. The weekly level of parasitism was estimated by taking random samples of at least fifty adult aphids from the windbreaks and dissecting them under a microscope. The number containing a parasite larva was noted.

In mid July of each season a random sample of five hundred leaves of A.glutinosa was taken from LF125 and WM110. The length and breadth of each were measured. Length and breadth are strongly correlated with area, the regression lines being fitted by:-

Length: $y = 9.25x-31.10$ $(r=0.904,\ p<0.001)$

Breadth: $y = 10.16z-24.74$ $(r=0.918,\ p<0.001)$

where y is the area (in cm^2), x the length and z the breadth of the leaf. Each week a random sample of twenty-five terminal and twenty-five non-terminal leaves was taken from each section of windbreak and their lengths and breadths measured. Using these two values the leaf area may be determined by reference to either of the regression lines. The two lines rarely give the same result for each leaf so the value used was the average of those derived for width and length, a procedure previously adopted with sycamore leaves by Dixon (1966). The leaf area values were used to assess the population density of the aphid.

At Lyne a different sampling technique was employed. Here four branches (one per tree) and one complete young tree (1.6m high) were selected and every leaf upon them examined weekly during 1982 and 1983. The same categories of aphids and natural enemies were counted as at East Malling.

PLATE 2

Mummified aphid carcasses produced by T.pallidus

(a) Aptera

(b) Alata

The young tree, hereafter referred to as 'the bush' and two of the branches (designated '1' and '2') were of A.glutinosa, the other two branches (designated '3' and '4') were on two A.hybrida trees. The trees present of A.incana and A.cordata were larger (about 4.3m) and the random 200 leaf sample technique was employed for these. Such complete samples were taken in order to assess the changes in aphid numbers within and between the individual trees in one locality. The number of leaves upon each branch and the bush was noted on each sampling occasion.

Using the counts of all aphids per leaf the variance (S^2) of the aphid distribution between leaves was related to the mean by the power law (Taylor,1961).

$$S^2 = a\bar{x}^b$$

where $\bar{x}$ is the mean number of aphids per leaf and a is a constant. This relationship may be expressed as a regression equation of the form

$$\log S^2 = \log a + b \log \bar{x}$$

where b is the index of aggregation of the species (Taylor,1961). Calculation of b requires several estimates of S^2 and $\bar{x}$ and therefore b cannot be calculated for one sample. Thus b was calculated for the sample set for a whole season. The parameter b is apparently independent of n, $\bar{x}$ and $\sum x$ and is less than one for a regular distribution, equal to one for a random distribution and greater than one for a contagious (aggregated distribution). To examine the dispersion weekly, Morisita's index was used. This is evaluated by

$$Id = n\frac{\sum(x^2) - \sum x}{(\sum x)^2 - \sum x}$$

(Morisita, 1959).

This index is a strong function of sample size (n) at both ends of its range. Morisita (1959) investigated changes in Id with the size of the sampling unit. It was found that when dispersion is contagious and individuals are randomly distributed in each clump, Id is fairly stable

until clump size and sample unit are approximately equal. As aphid distributions are often aggregated (Dixon,1966; Wratten, 1974; Lorriman,1980) and the sampling units were always greater than clump size, this measure was used as a comparative index.

2.2.3. Meteorological data

Meteorological records were collected from both sites. At Lyne maximum and minimum temperature readings were taken twice weekly. For East Malling data from the meteorological station on site was used.

This section describes the results of the detailed sampling at the two sites. Data from the natural situation at Lyne are considered first, followed by that from the managed windbreaks at East Malling.

2.3 RESULTS AT LYNE

2.3.1, 1982

(i) Abundance of aphids

Weekly leaf counts taken gave the sampling unit size for each branch (fig.2a,b). New leaves continued to grow until mid July. However, from late June onwards older leaves were shed, in small numbers at first, the process accelerating as summer advanced. Thus the leaf curves tend to level out in late June, the increment to the branch being cancelled out by the shedding process. When growth stops the shedding becomes apparent and the curve begins to fall. Leaves were shed green with few apparent signs of senescence.

Overwintering eggs hatched in late April to give apterous fundatrices. Numbers rose rapidly during May on the bush and all branches (fig.3a,b,c,d,e). The pattern of abundance was similar although numbers varied between the trees (table 1). Except for branch 3 the populations showed a drop in the middle of the build up. For branches 1, 4 and the bush this occurred

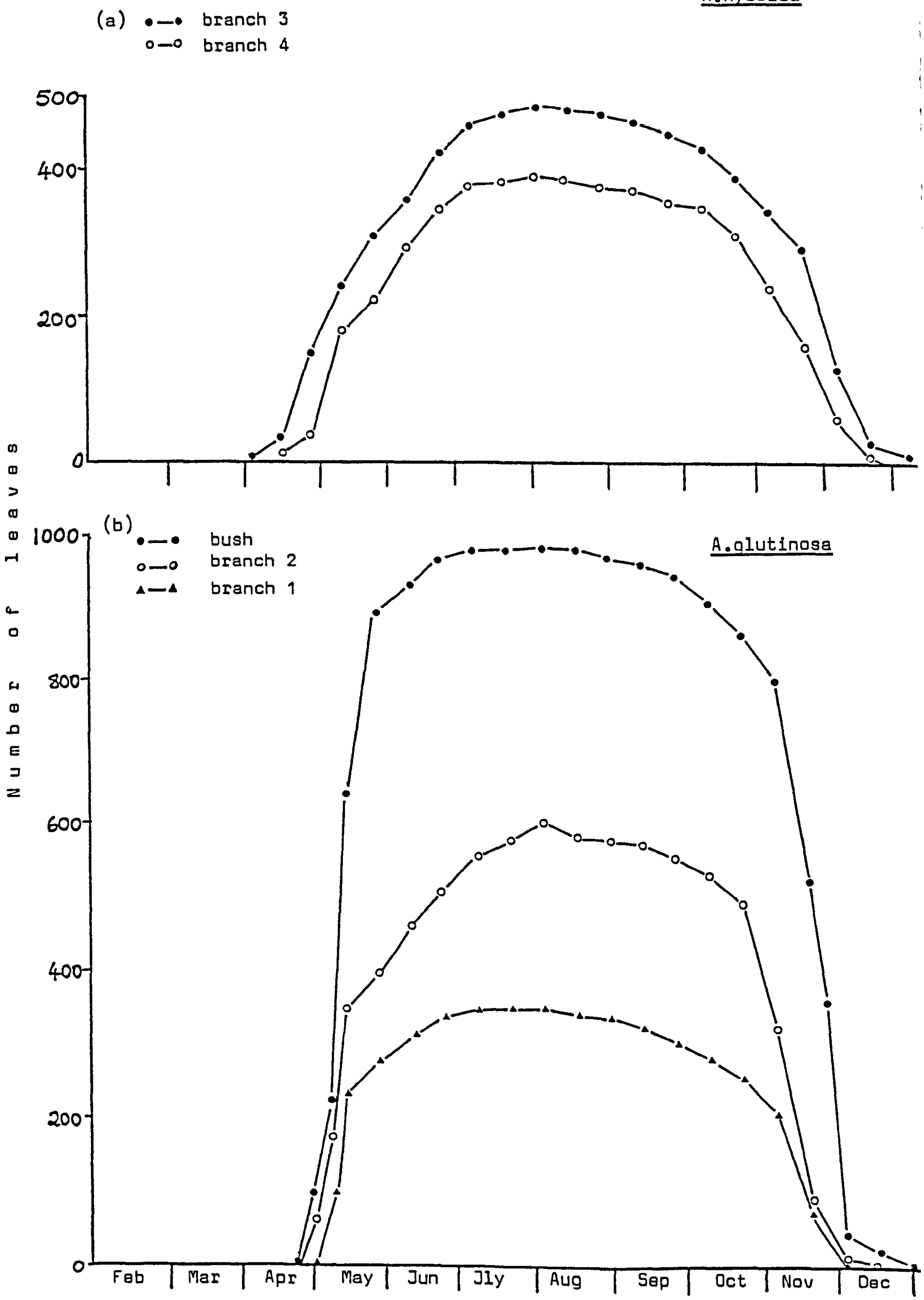


Figure 2: Leaf counts for sampled branches and bush at Lyne, 1982

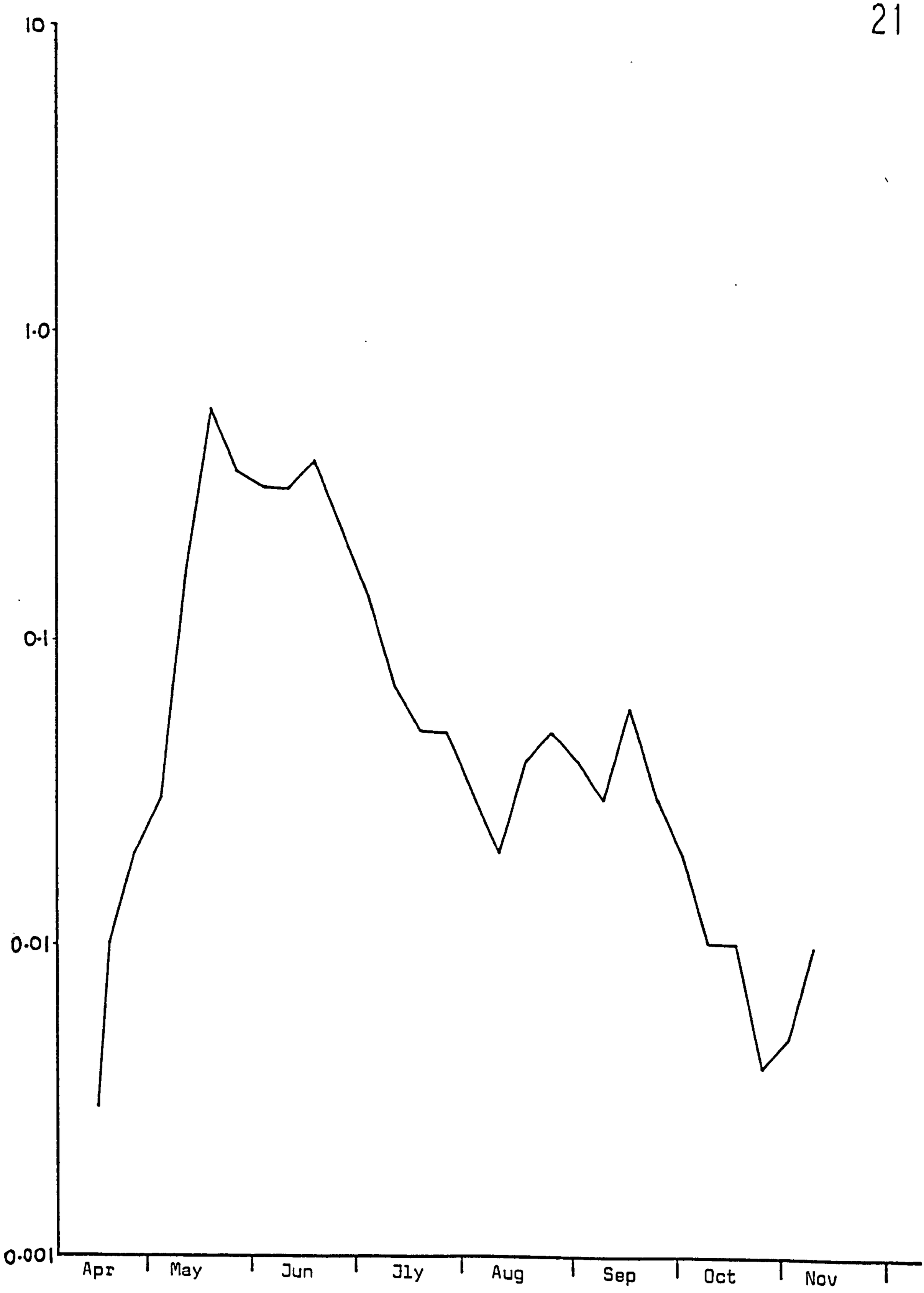


Figure 3 (a): Aphid population, Branch 1, 1982

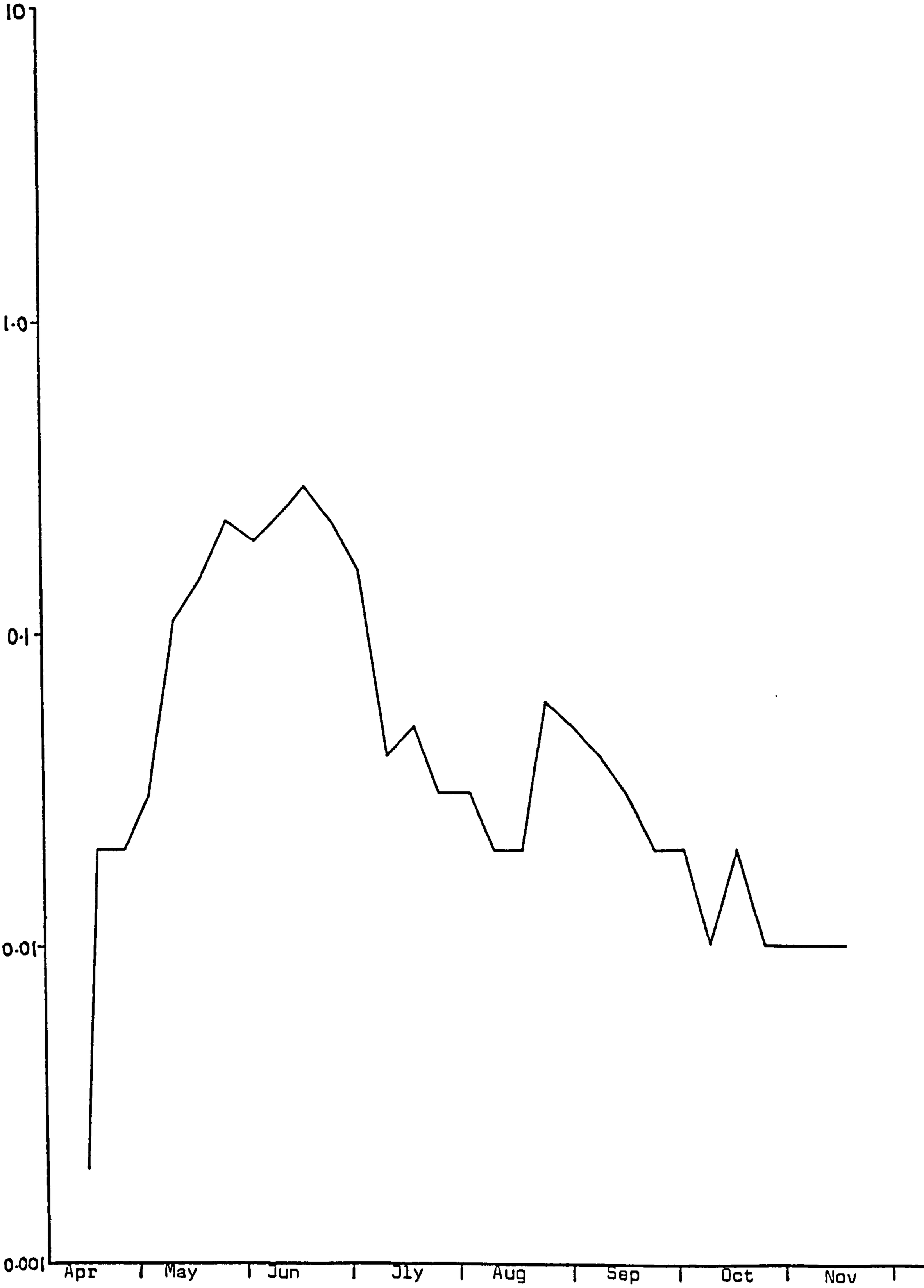


Figure 3 (b): Aphid population, Branch 2, 1982

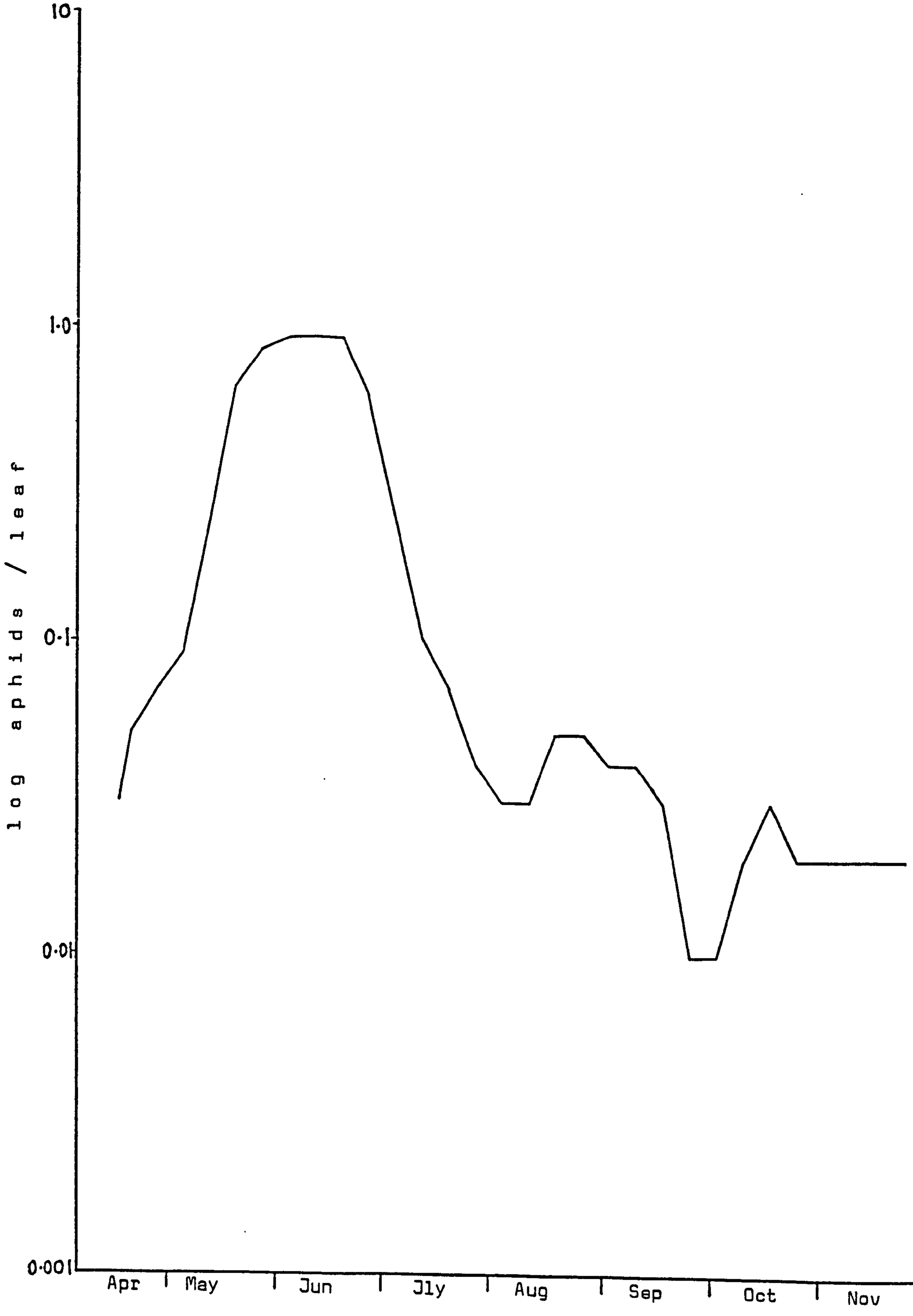


Figure 3 (c): Aphid population, Branch 3, 1982

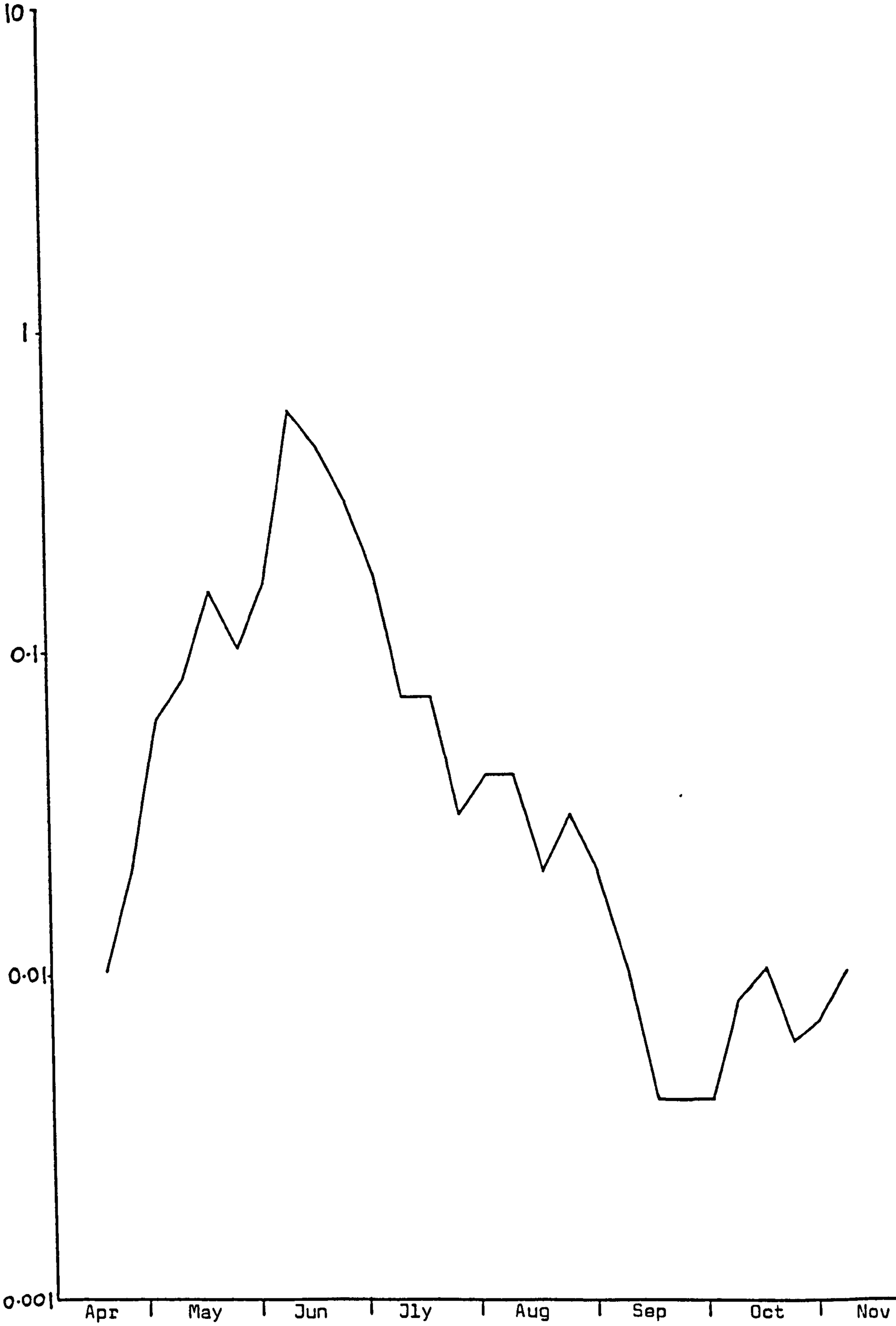


Figure 3 (d): Aphid population, Branch 4, 1982

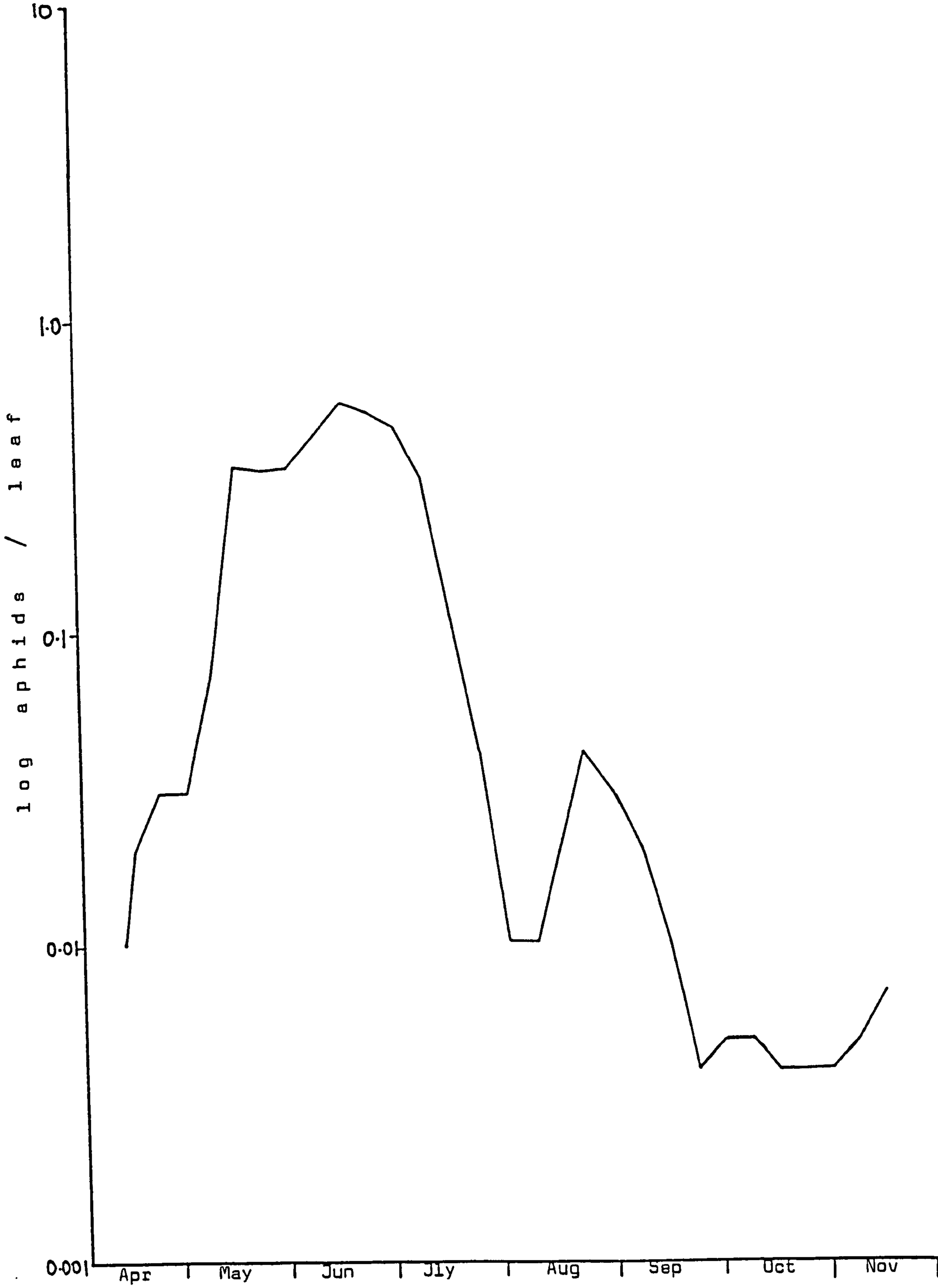


Figure 3 (e): Aphid population, the bush, 1982

Table 1 TOTAL APHIDS PER BRANCH - LYNE 1982

Date		Branch 1	Branch 2	Branch 3	Branch 4	Bush
April	15	0	0	0	0	0
	19	1	1	7	0	9
	21	4	8	15	3	15
	28	7	10	23	6	24
May	5	8	13	33	19	25
	12	50	54	96	27	66
	19	182	78	276	51	331
	26	118	124	377	36	321
June	2	113	112	428	55	335
	9	108	134	436	209	415
	16	132	175	440	160	542
	23	81	139	293	110	507
	30	47	93	115	65	438
July	7	25	24	48	27	301
	14	18	29	36	26	121
	21	16	15	20	10	42
	28	9	15	12	16	13
Aug	4	5	11	12	14	6
	11	14	13	23	6	21
	18	17	33	22	12	36
	25	14	28	20	7	28
Sept	1	10	19	17	4	21
	8	17	17	12	1	8
	15	10	10	6	1	3
	22	6	9	5	1	3
	29	3	5	8	2	3
Oct	6	4	9	12	3	2
	13	1	5	8	1	2
	20	1	4	7	1	2
	27	1	3	5	1	2
Nov	3	0	1	3	0	2
	10	0	1	2	0	0
	17	0	1	2	0	0

between May 19th and 26th and for branch 2 between May 26th and June 2nd. This period was a time of intense thundery activity with frequent and heavy downpours. One such cloudburst resulted in the site being flooded to a depth of 1 metre. This meant that for a few hours branch 1 was under water. It is likely that this caused the dramatic drop in numbers. The population recovered but did not reach the level attained earlier, thus the recorded peak is very much earlier than the other branches and probably represents a situation caused by extreme local weather conditions. The drop on other branches was considerably less than that for branch 1 and did not appear to affect the populations which continued to increase and peak later in the season. The cause of this drop in the populations appears to be due to a loss of young nymphs. Nymphs may be dislodged more easily during periods of heavy rain and this would account for this occurrence. The population on branch 3 did not decrease although the number of nymphs did not increase considerably. At the beginning of this period (May 19th) there were considerably more adults present on this branch and this would have resulted in more nymphs being produced. This may have cancelled out the loss caused by rain.

Apart from branch 1 the populations peaked mid June and declined during July. There were small resurgences in September and early October. Only occasional alates were recorded during July on A.incana and A.cordata and overall these trees did not support any aphid populations.

The age structure of the populations indicated that throughout the season instars I-III formed over 60% of the population and during the period of maximum abundance they accounted for 70-80% of total numbers (fig.4;a,b,c,d,e The decline in the total population was mirrored by a similar decline in numbers of these young nymphs. After the peak these instars continued to account for about 80% of the population but the proportion of older instars increased towards the end of the season. Due to the fact that so much of the population is of this age group, the overall changes are largely a result

Figure 4 (a)

Age structure of the population on branch 1, 1982

(i) Alate adults

(ii) Fourth instars (presumptive alatae

(iii) Apterous adults

(iv) Fourth instars (presumptive apterae)

(v) Nymphs

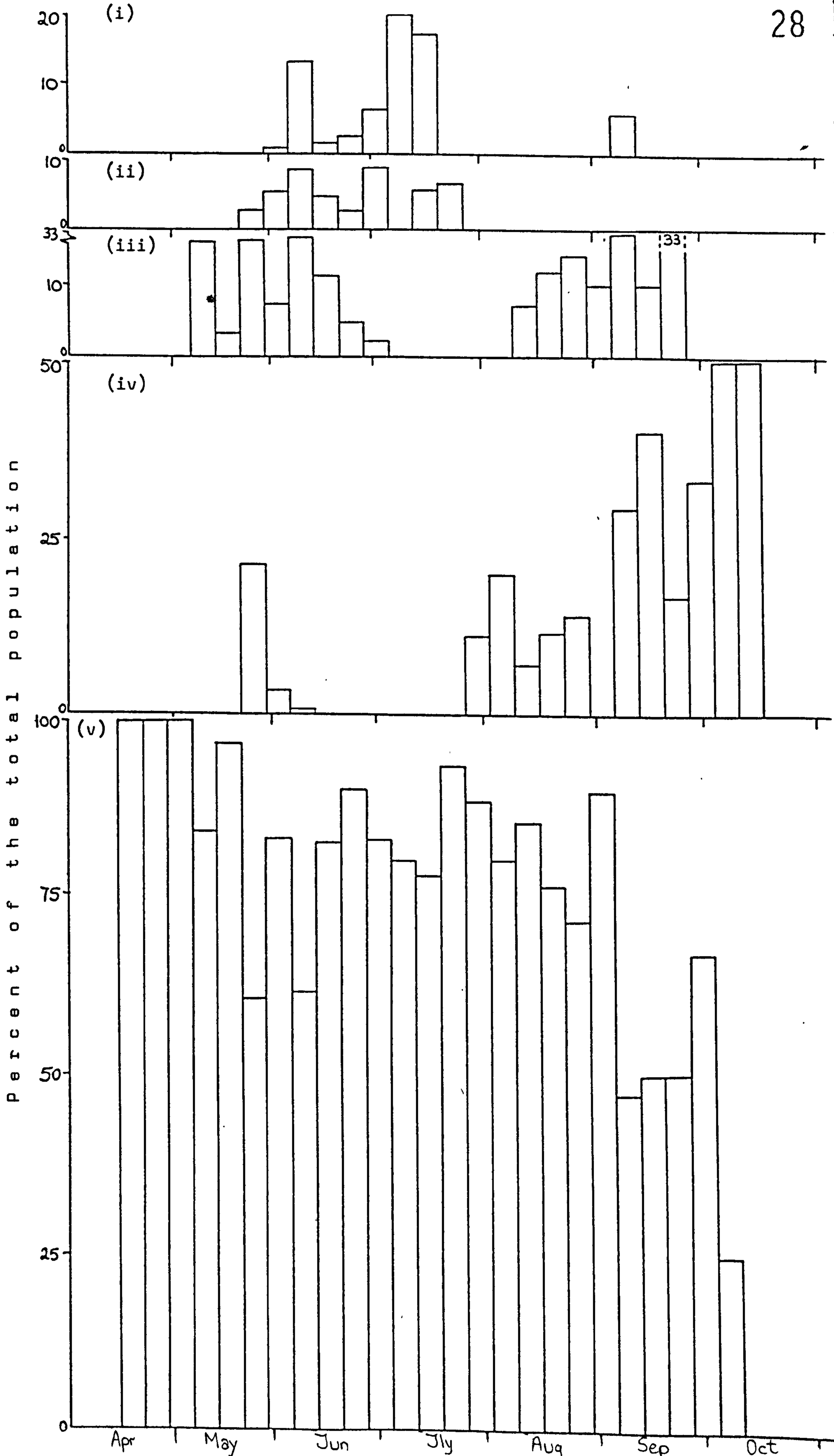

(i)
20
10
0
(ii)
10
0
(iii)
33
10
0
33
(iv)
50
25
0
(v)
100
75
50
25
0
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 4 (b):

Age structure of the population on branch 2, 1982

legend as for figure 4 (a)

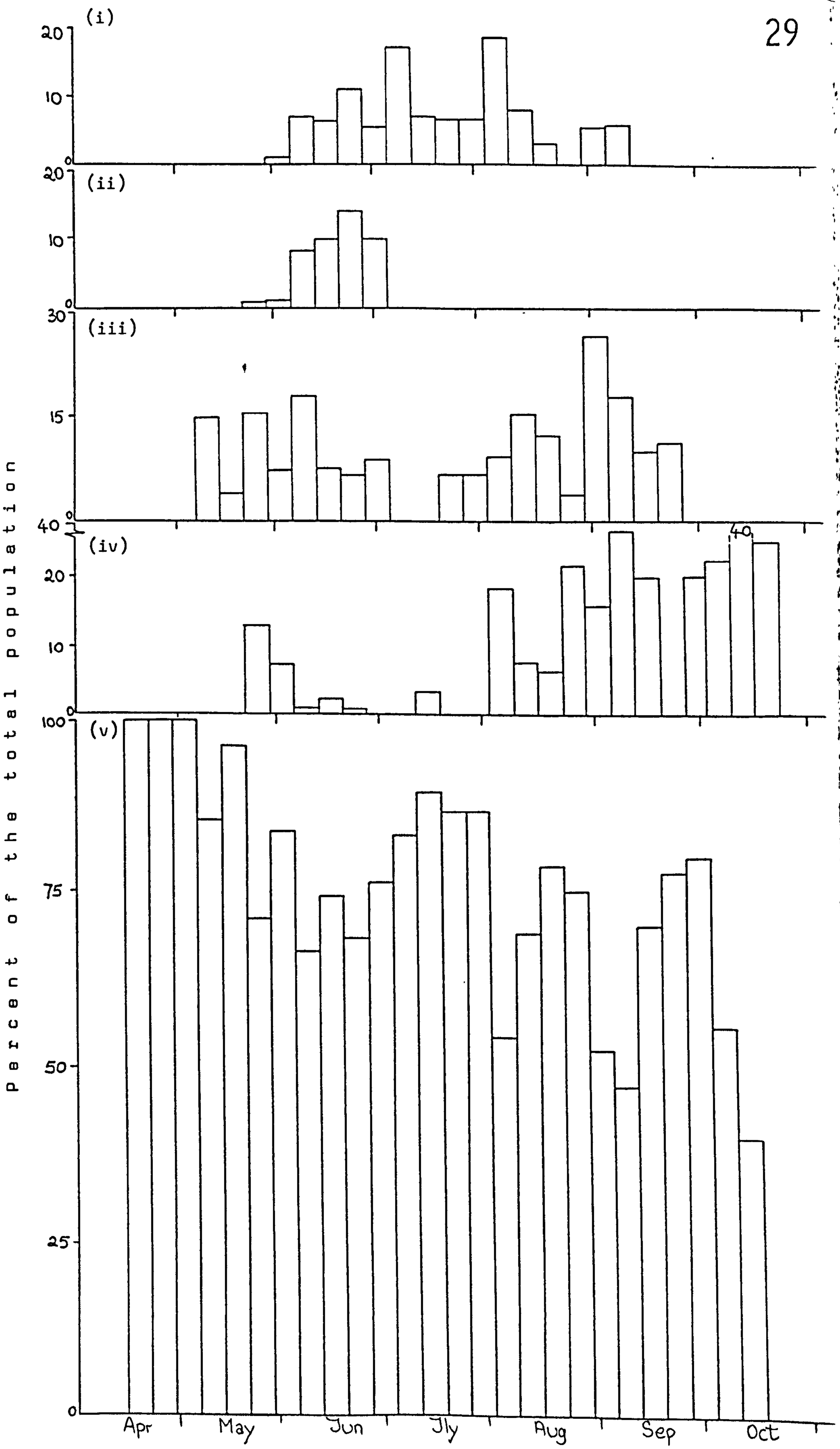

(i)
20
10
0
(ii)
20
10
0
(iii)
30
15
0
(iv)
40
20
10
0
(v)
100
75
50
25
0
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 4 (c):

Age structure of the population on branch 3, 1982

legend as for figure 4 (a)

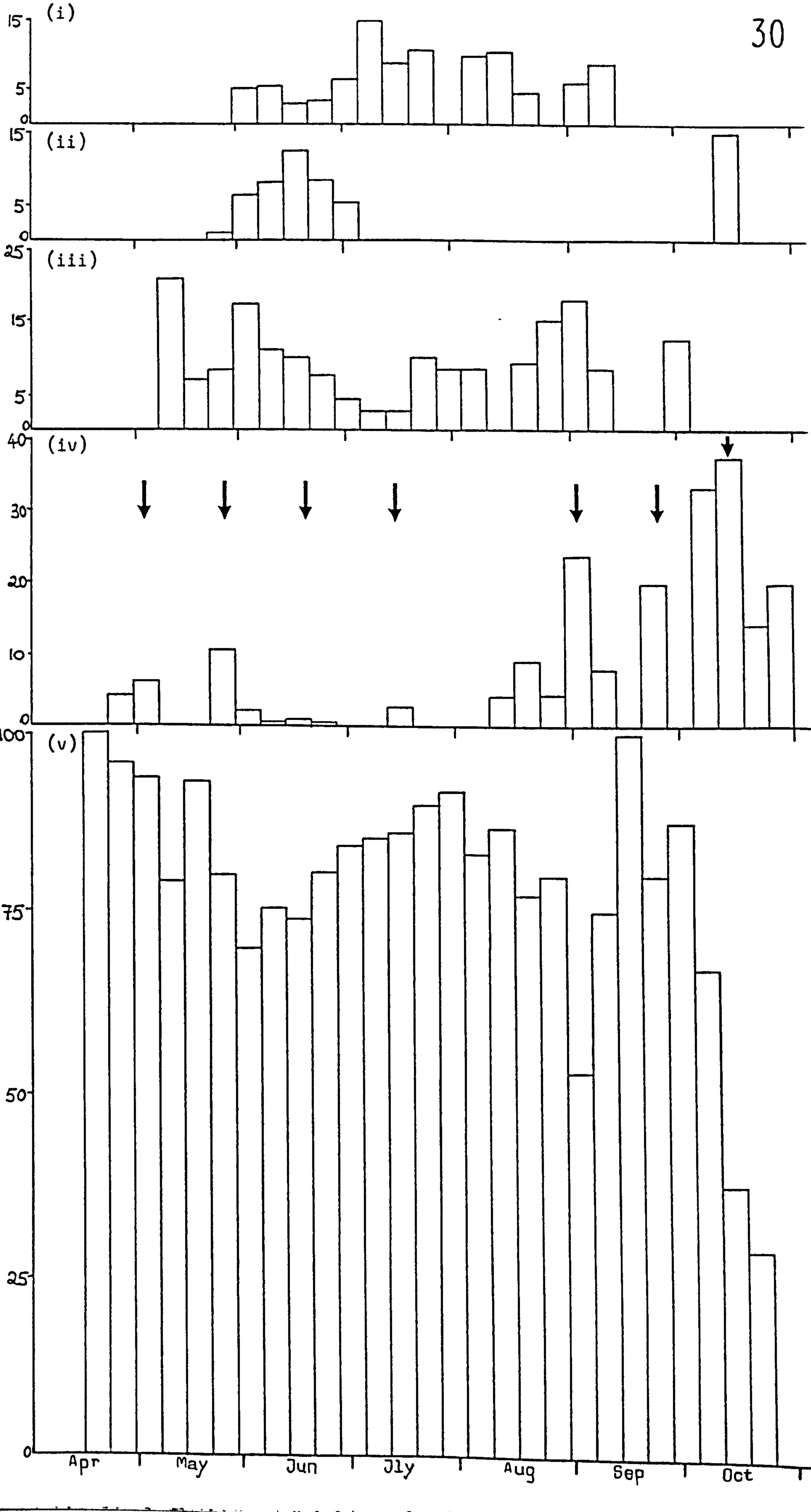

(i)
15
5
0
(ii)
15
5
0
(iii)
25
15
5
0
(iv)
40
30
20
10
0
(v)
100
75
50
25
0
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 4 (d):

Age structure of the population on branch 4, 1982

legend as for figure 4 (a)

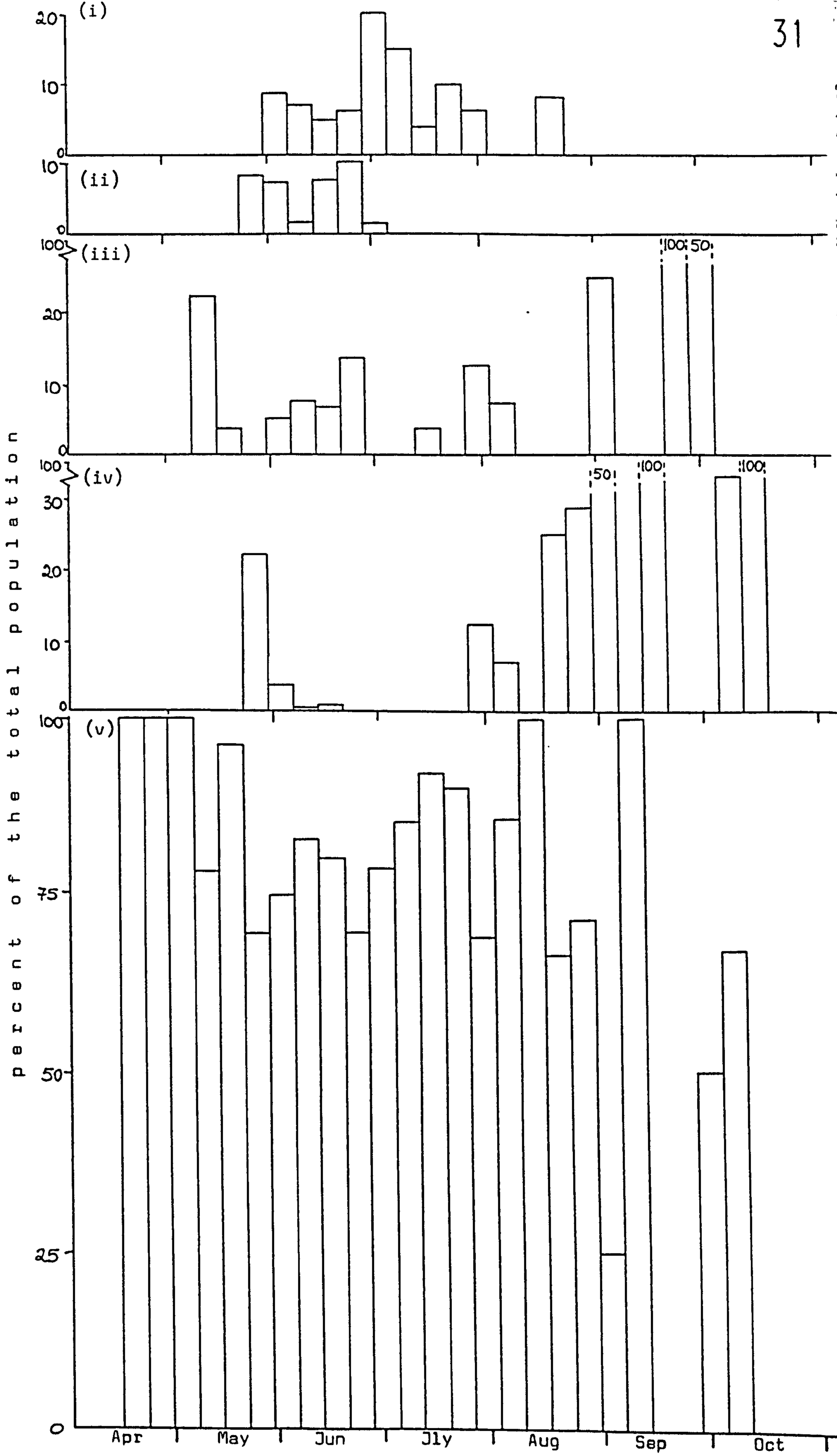
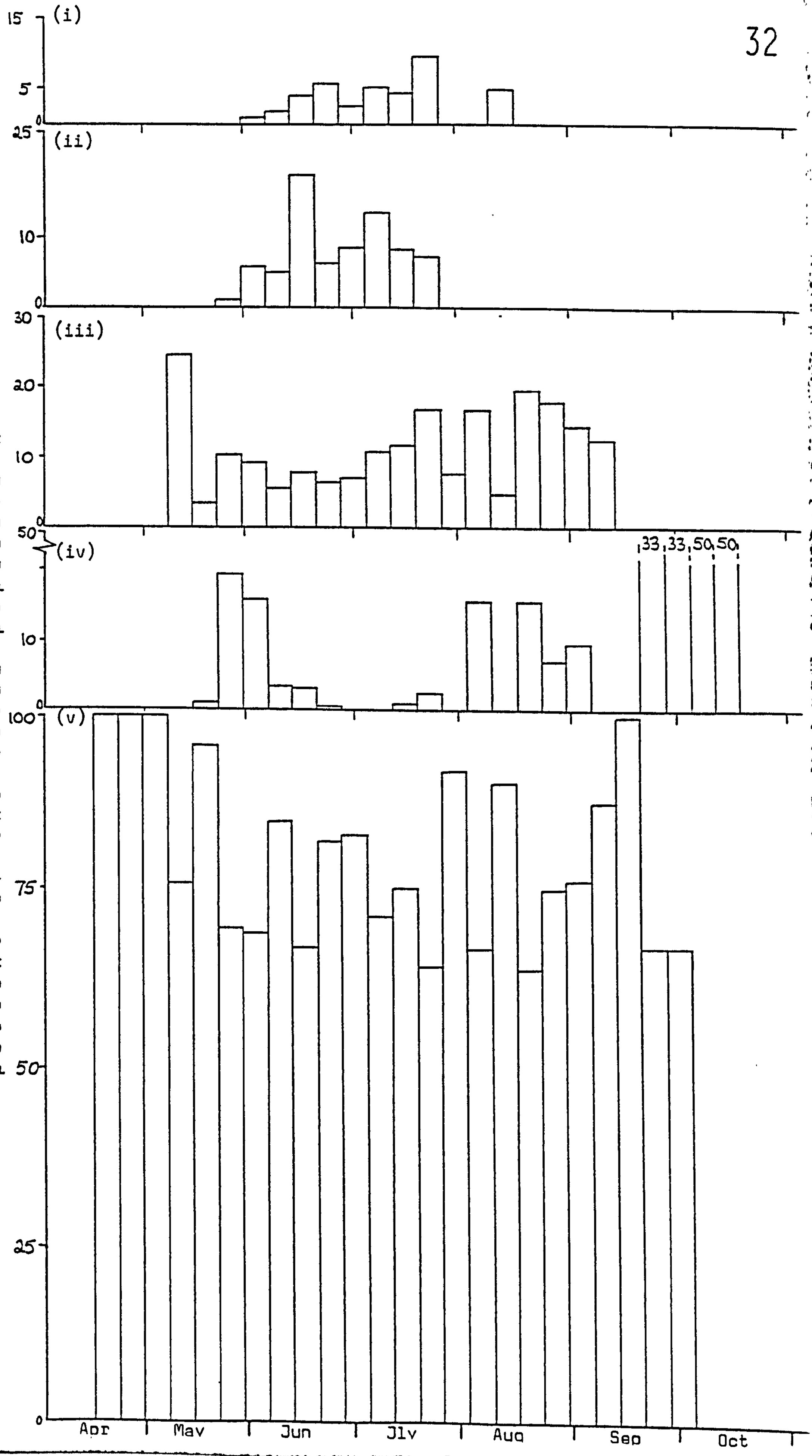

(i)
20
10
0
(ii)
10
0
(iii)
100
20
10
0
100
50
(iv)
100
30
20
10
0
100
50
100
100
(v)
percent of the total population
75
50
25
0
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 4 (e):

Age structure of the population on the bush, 1982

legend as for figure 4 (a)


(i)
15
5
0
(ii)
25
10
0
(iii)
30
20
10
0
(iv)
50
10
0
33
33
50
50
(v)
100
75
50
25
0
percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct

of changes in abundance of these nymphs. During the first weeks of the season the numbers of instars I, II and III were counted separately. This was abandoned as classification was difficult and possibly inaccurate and the procedure was very time consuming. When Hughes'(1962) test for a stable age distribution was applied to these samples the numbers did not appear to conform to a geometric series. This is similar to the findings of Milne (1971) and Perrin (1974). The method of Hughes applies only to populations which show a steady increase, such as the cabbage aphid (Hughes, 1963) although in this case it was not infallible. As stated by Carter, Aikman and Dixon (1978) it is virtually impossible for aphid populations to reach stability, because of the short period of time available and the variability of factors such as reproductive rates and age-specific mortalities. Populations of P.alni increase and decline over periods of ten to twelve weeks and do not show a steady increase.

The age structure histograms are useful because they establish the morph of the adult vivipara in each generation. If the relative proportions of the two presumptive morphs of the fourth instar nymphs are examined it provides an indication of the individuals being recruited to the adult stage. It is a feature of aphids that the generations overlap, thus any analysis of this kind will not be clear cut. However, the age structure of branch 3 provides a good example (fig.4,c). The first generation was apterous, shown by the early peak of fourth instars (presumptive apterae) and subsequent viviparae. The second generation was mostly apterous and the third generation almost entirely alate. No alates were produced in subsequent generations, there being no further records of fourth instars (presumptive alatae). The fourth, fifth and sixth generations were entirely apterous and the peaks on the alate graph were caused by isolated specimens arriving on the branch, having migrated from elsewhere. The large peaks late in the season of fourth instars were presumptive males (alatae) and oviparae (apterae). Other branches show a similar age

distribution and P.alni appears to have had seven generations at this site in 1982.

Winged adults first appeared in late May . There were no significant differences between the proportions of fourth instar (presumptive alatae) on each branch; all d values being less than 1.96 (5% level) for the test of proportions (Bailey, 1959). The data was thus averaged and is shown in fig.5. The proportion rose rapidly and on July 7th all the fourth instar were presumptive alatae. Alate nymphs continued to be produced until late July.

Sexual forms appeared from late September onwards (fig.6). Few males were found but their appearance preceded that of oviparae, which appeared in early October. No males were found from mid October onwards but oviparae often persisted until leaf fall in late November. On days in early December leaves which had recently fallen were found on the ground with live oviparae still upon them. Most oviparae appeared to mature at a similar time and numbers slowly decreased as autumn advanced (fig.7).

(ii) Spatial distribution of aphids

The value of b in Taylor's power law was significantly greater than 1 on all branches and the bush for the season as a whole, indicating that the aphid distribution was aggregated, (table 2). Only when mean values were small, that is when the population was low, was the variance less than or equal to the mean. This indicates that the dispersion was regular and is confirmed by the value of Morisita's index being 0 for the beginning and end of the season (table 3). A value of 0 is obtained by $\sum x$ being equal to $\sum x^2$, i.e. there being one aphid per leaf. Thus when the aphids hatch in the spring or are present in low numbers in autumn they tend to be distributed one per leaf. A typical plot of variance against mean (that for the bush) is given in fig.8. All other plots were very similar,

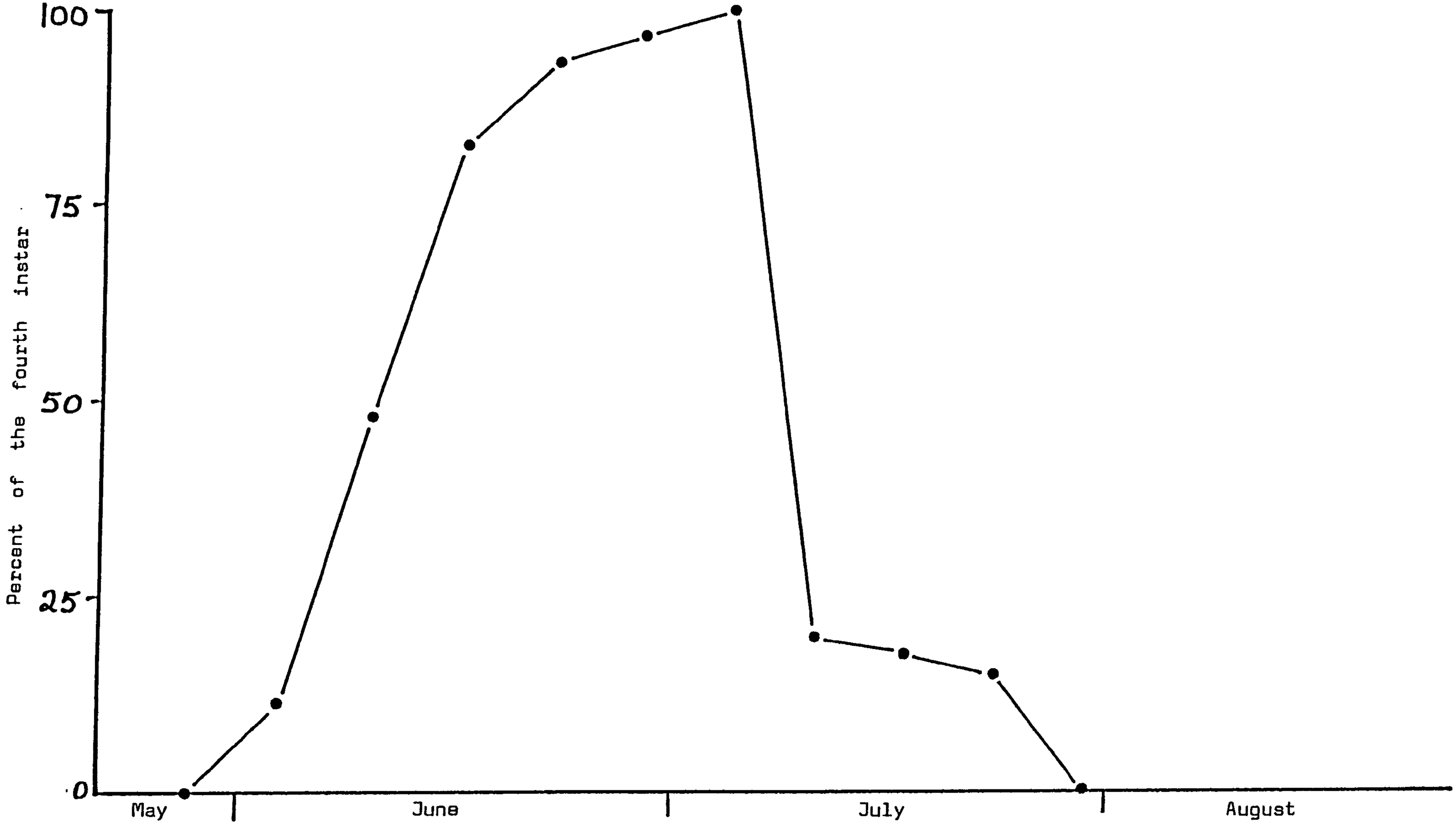
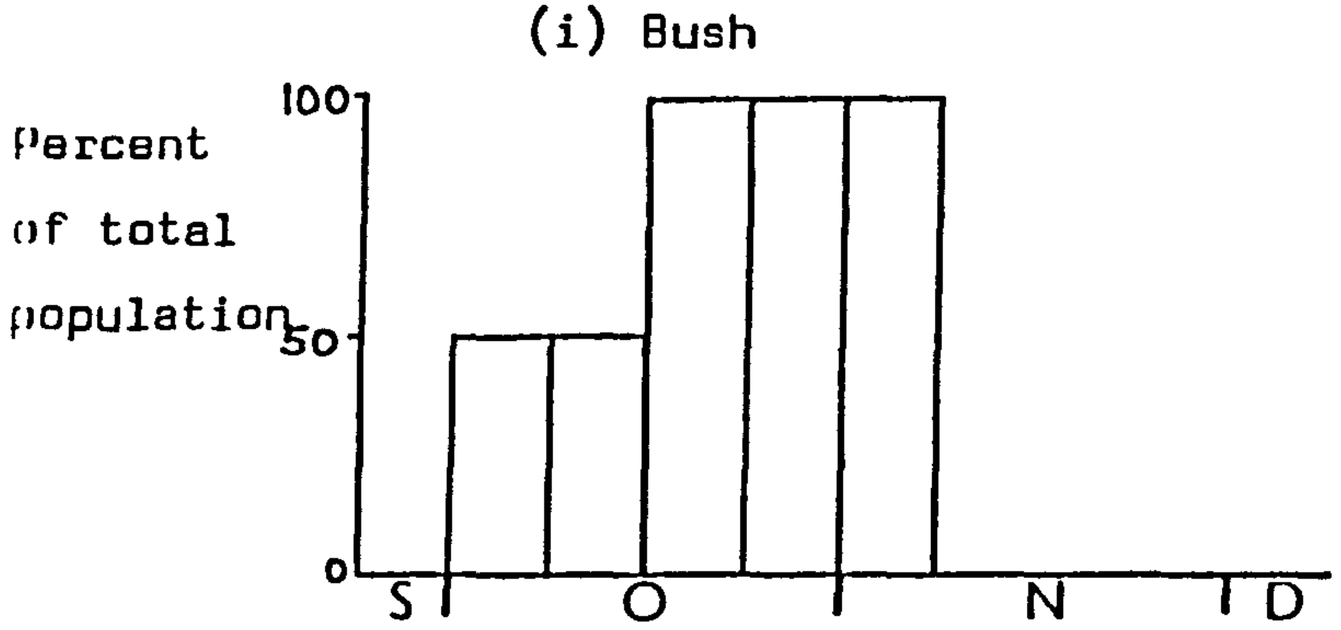
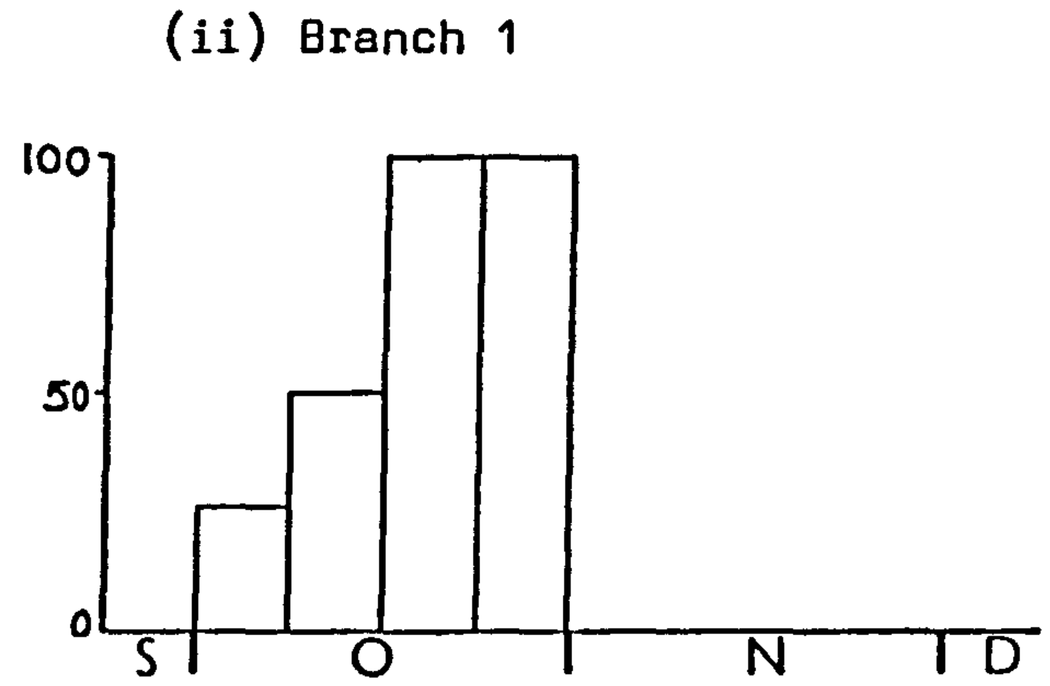
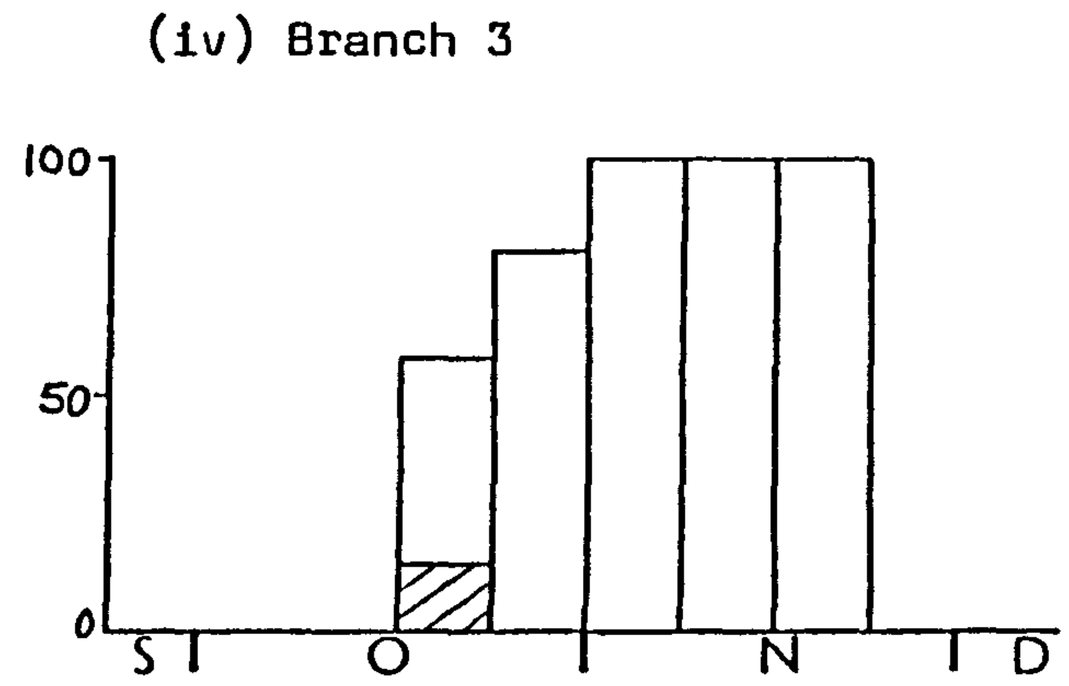
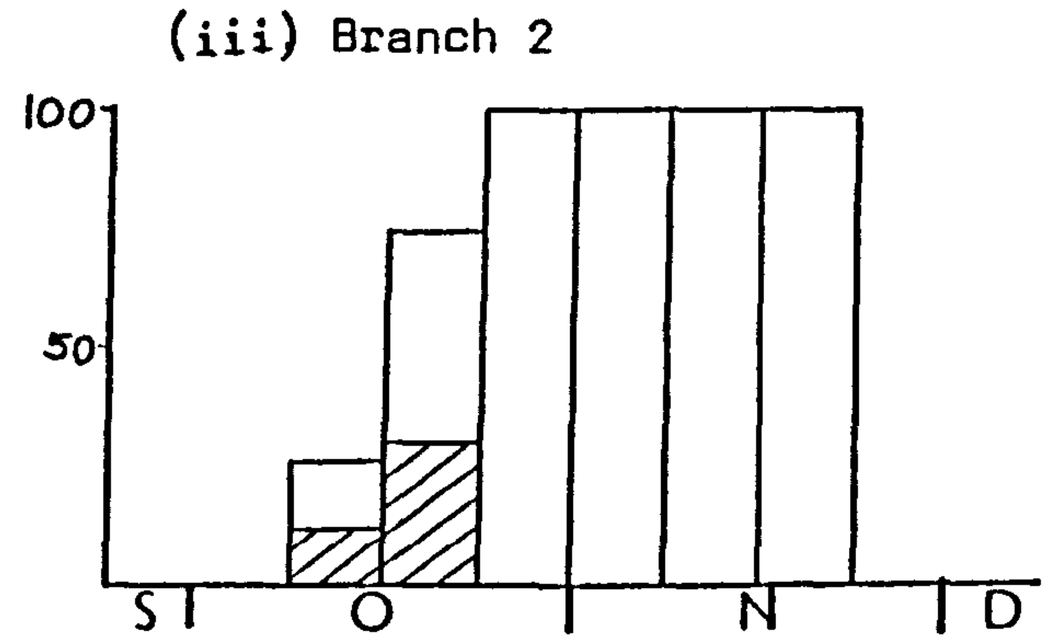


Figure 5: Proportion of presumptive alatae in the fourth instar, all branches, 1982 at Lyne









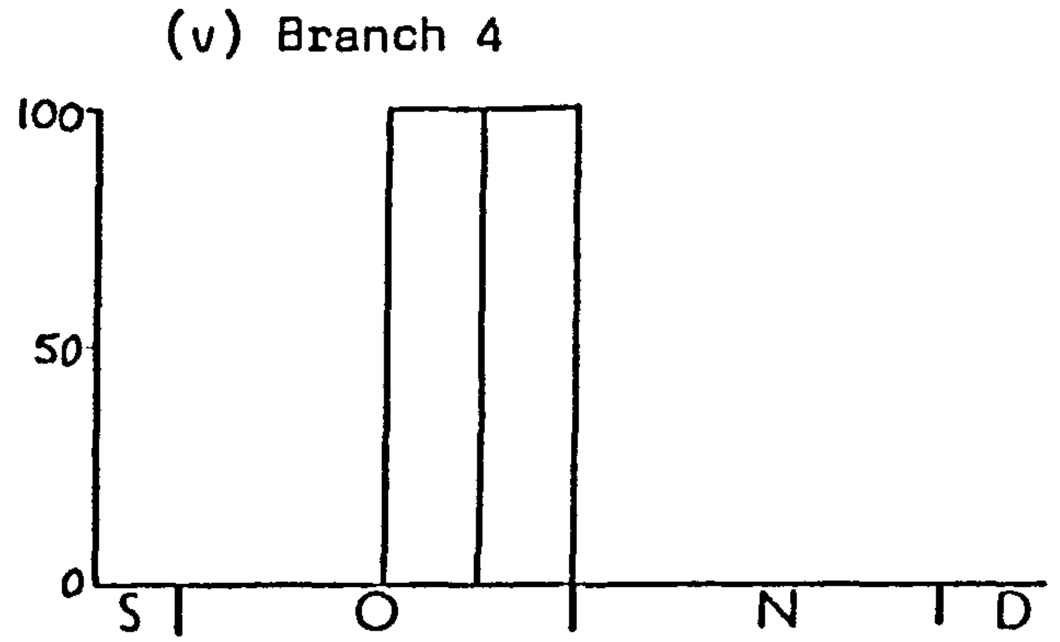
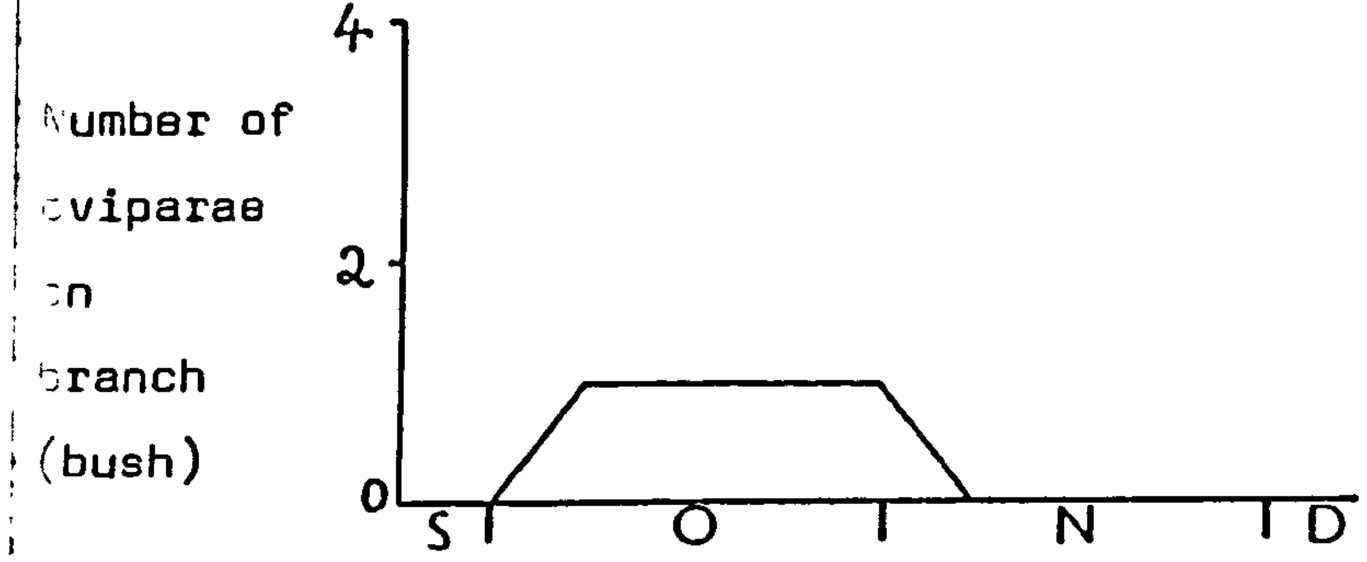


Figure 6: Appearance of sexuales, Lyne 1982

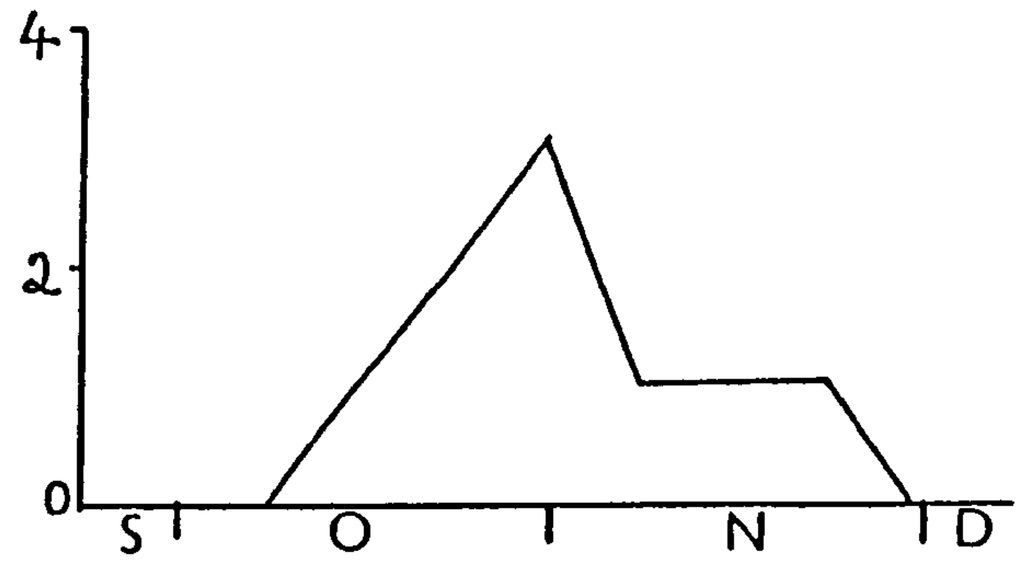
Oviparae

Males

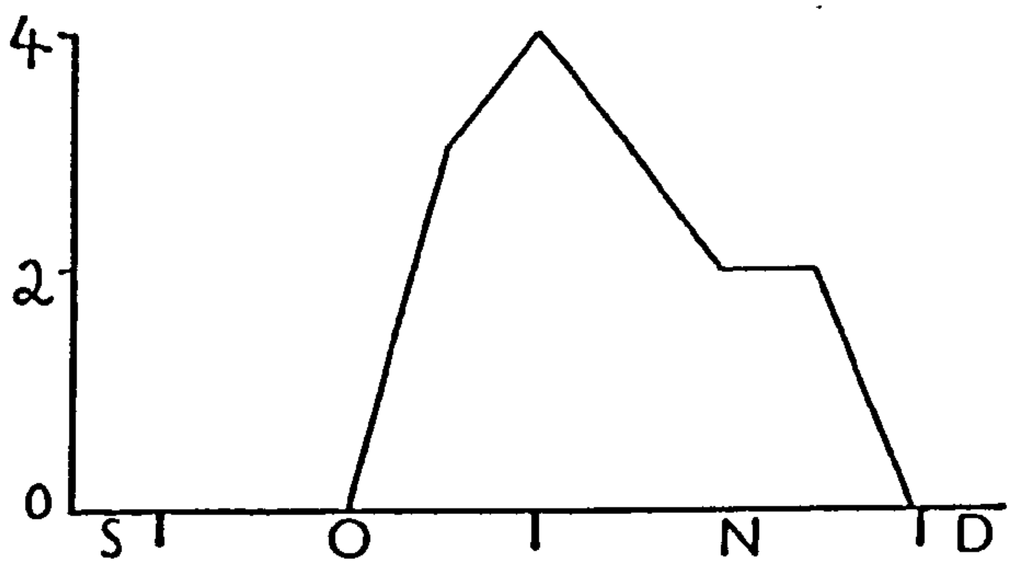
(i) Branch 1



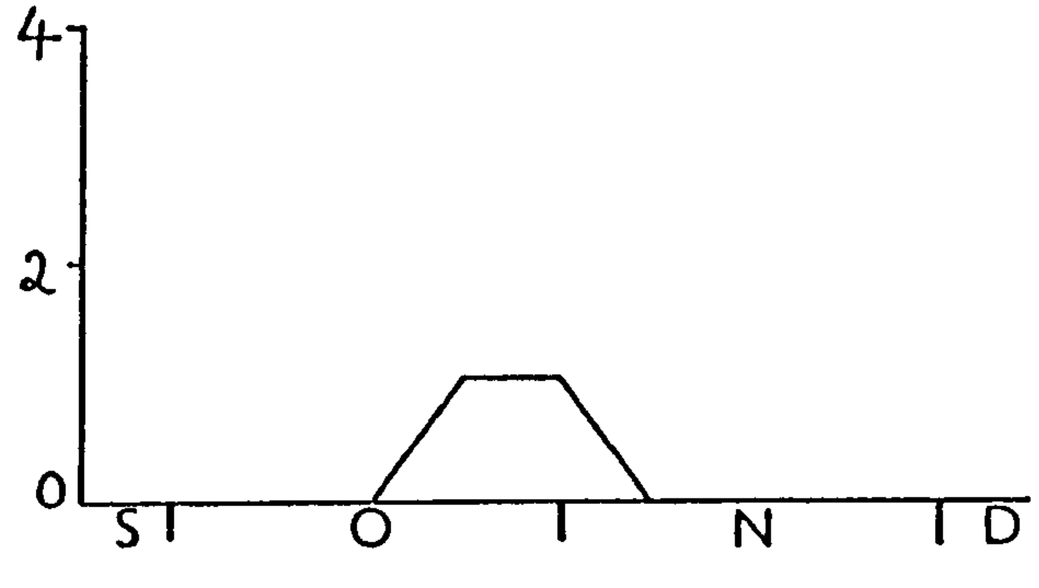
(ii) Branch 2



(iii) Branch 3



(iv) Branch 4



(v) Bush

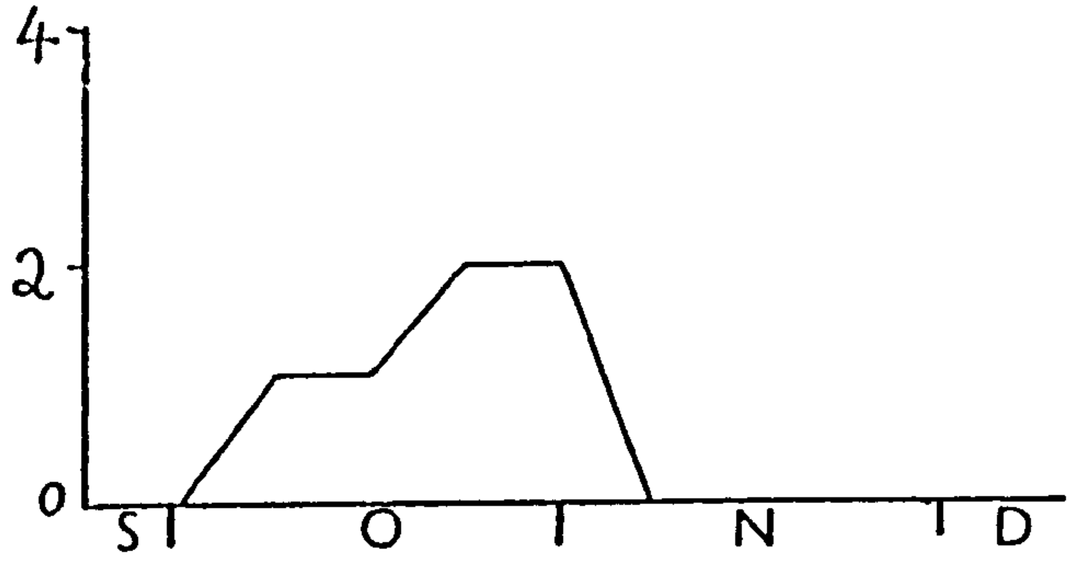


Figure 7: Numbers of oviparae, Lyne, 1982

Table 2 REGRESSION PARAMETERS OF LOG S^2 ON LOG $\bar{X}$, LYNE 1982 & '83

1982

Branch	b	± St.Error	a
1	1.364	0.0551	5.271
2	1.326	0.0814	4.819
3	1.363	0.0695	4.711
4	1.242	0.0408	3.396
bush	1.364	0.0458	7.340

1983

Branch	b	± St.Error	a
1	1.493	0.0879	8.944
2	1.339	0.0697	5.082
3	1.333	0.0522	5.455
4	1.389	0.0556	6.043
bush	1.426	0.0562	12.335

All values of b are significantly different from 1 at $p < 0.001$

Table 3 MORISITA'S INDEX OF DISPERSION , LYNE 1982

Date		Branch 1	Branch 2	Branch 3	Branch 4	Bush
May	26	11.9	12.8	6.8	8.2	18.0
June	2	10.3	9.8	6.8	25.0	9.8
	9	5.9	10.2	8.2	6.5	9.6
	16	6.4	9.4	3.7	5.1	6.6
	23	5.1	13.1	5.1	3.5	10.9
	30	4.5	6.7	5.4	3.8	14.8
July	7	3.5	6.5	2.6	12.0	64.1
	14	13.5	8.6	3.8	1.2	15.9
	21	5.7	0.0	0.0	0.0	18.1
	28	28.4	120.7	107.7	34.4	12.4
Aug	4	0.0	31.4	42.8	20.4	64.3
	11	39.9	21.9	27.6	0.0	128.0
	18	19.4	55.5	2.0	33.1	10.6
	25	21.2	17.8	0.0	0.0	12.5
Sept	1	13.7	3.2	3.2	0.0	8.8
	8	17.1	4.0	26.2	0.0	0.0
	15	19.3	11.9	0.0	0.0	0.0
	22	18.6	0.0	0.0	0.0	0.0
	29	0.0	0.0	0.0	0.0	0.0
Oct	6	0.0	125.0	0.0	0.0	0.0
	13	0.0	0.0	0.0	0.0	0.0
	20	0.0	0.0	0.0	0.0	0.0
	27	0.0	0.0	0.0	0.0	0.0

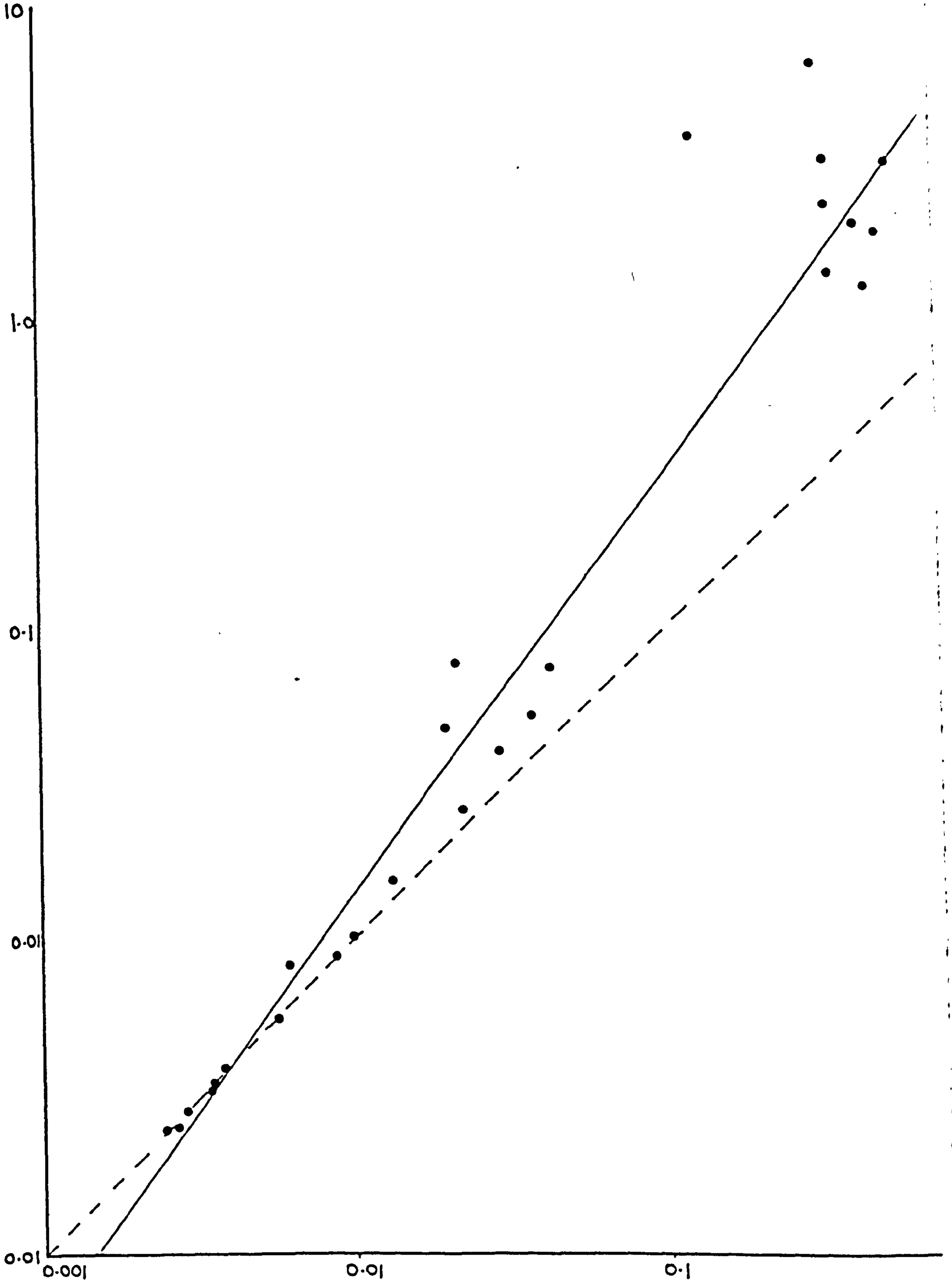


Figure 8: Relationship between log. mean and log. variance of aphid distribution, the bush, 1982

shown by the similarity of the values of b in table 2.

The value of Morisita's index after initially being zero increased rapidly early in the season (table 3), coinciding with the onset of reproduction by the fundatrices. It fell and remained at a relatively low level during population build up. After the peak it assumed high values again as the population became 'patchy' with the onset of reproduction by subsequent generations of viviparae. Finally, when the numbers were low in autumn the index became zero again as the aphids present were generally one to a leaf. (Appendix 1.1,1.2,1.3).

(iii) Abundance of natural enemies

The total numbers of predators found on each branch are shown in fig.9. As the aphid population increased dramatically the ratio of predators to aphids fell in mid summer being highest in late summer (fig.10).

The first predators recorded were Anthocoris nemorum L. and A.nemoralis Fabricius. These overwinter as adults and appeared on the alder in late May. A.nemoralis was found only occasionally. The coccinellid Adalia bipunctata L. which also overwinters as an adult arrived in late May and larvae were found in early June. This was the only coccinellid found during the year. Of the Heteroptera, Psallus ambiguus Fallen was first recorded as nymphs in early June and adults appeared towards the end of the month. None were found after mid July. The commonest predator was B.angulatus, comprising 54% of total numbers recorded (fig.11). Nymphs of this bug appeared in mid June and these produced adults by mid July. Numbers declined in late July (fig.12), but females persisted through August. The pentatomid bug, Pentatoma rufipes L. was also found occasionally but in such small numbers as to exert little effect on the aphid population. It is not clear whether or not this bug is carnivorous (Southwood and Leston,1959).

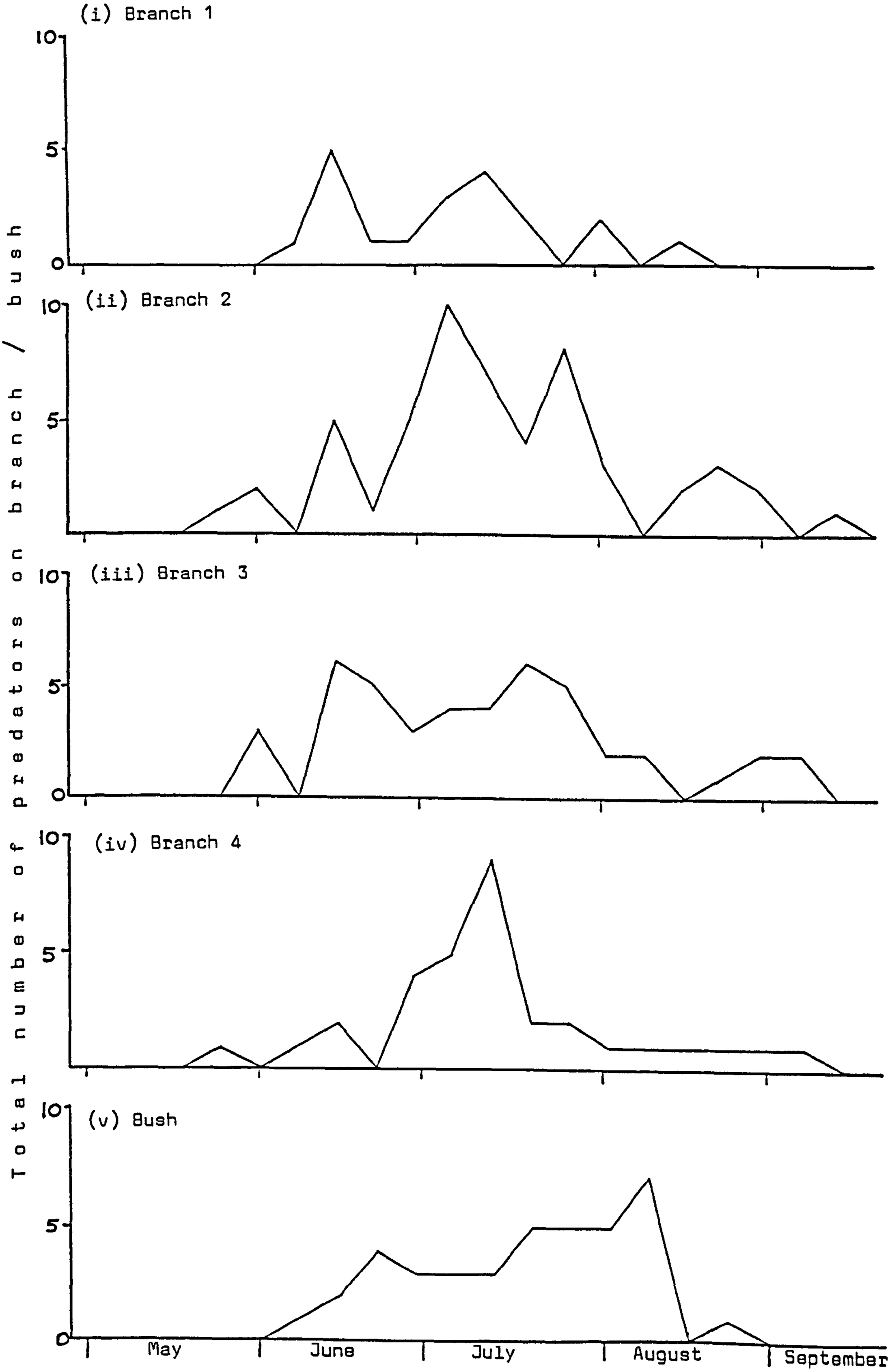


Figure 9: Total numbers of predators during 1982 at Lyne

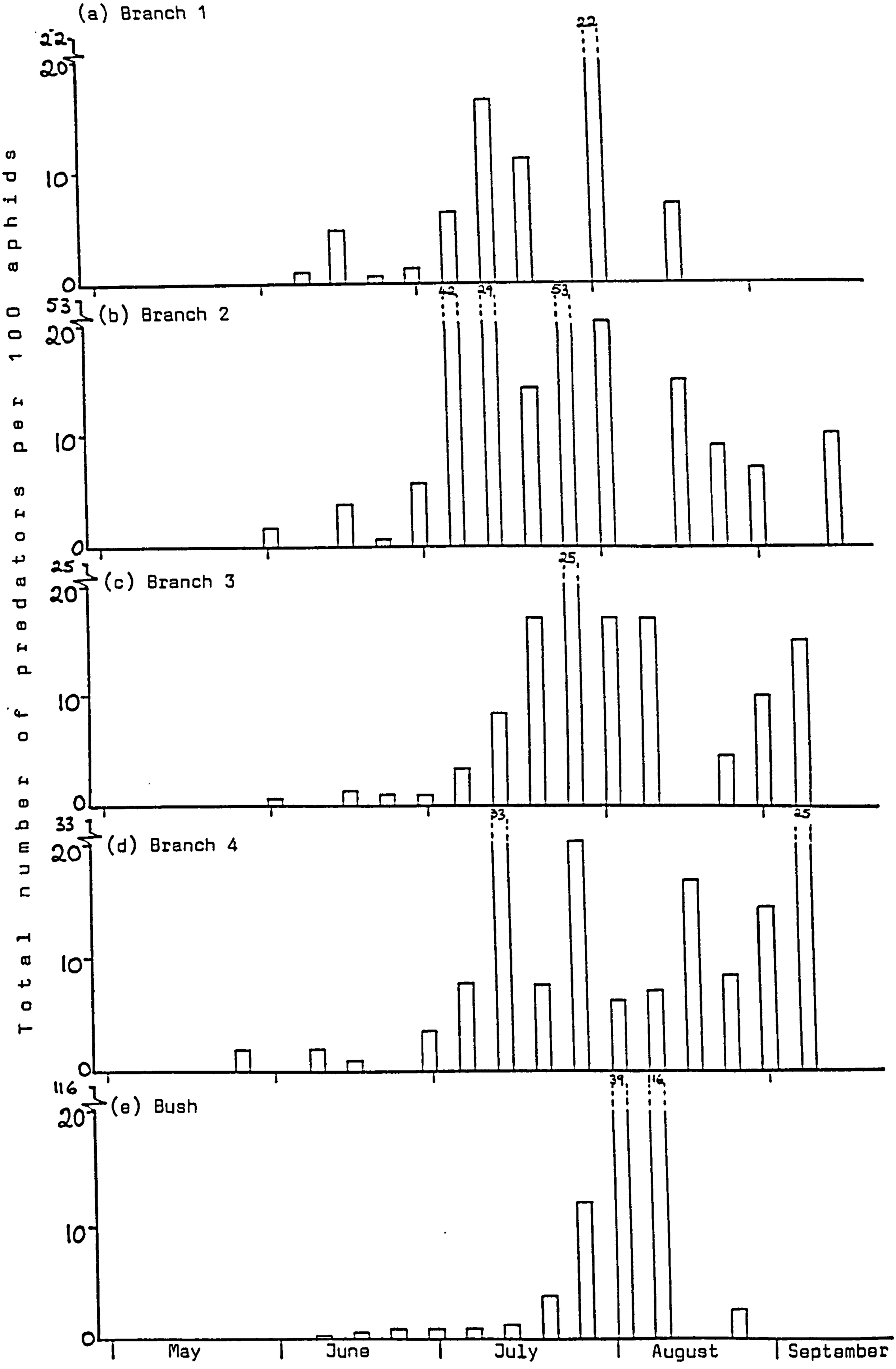
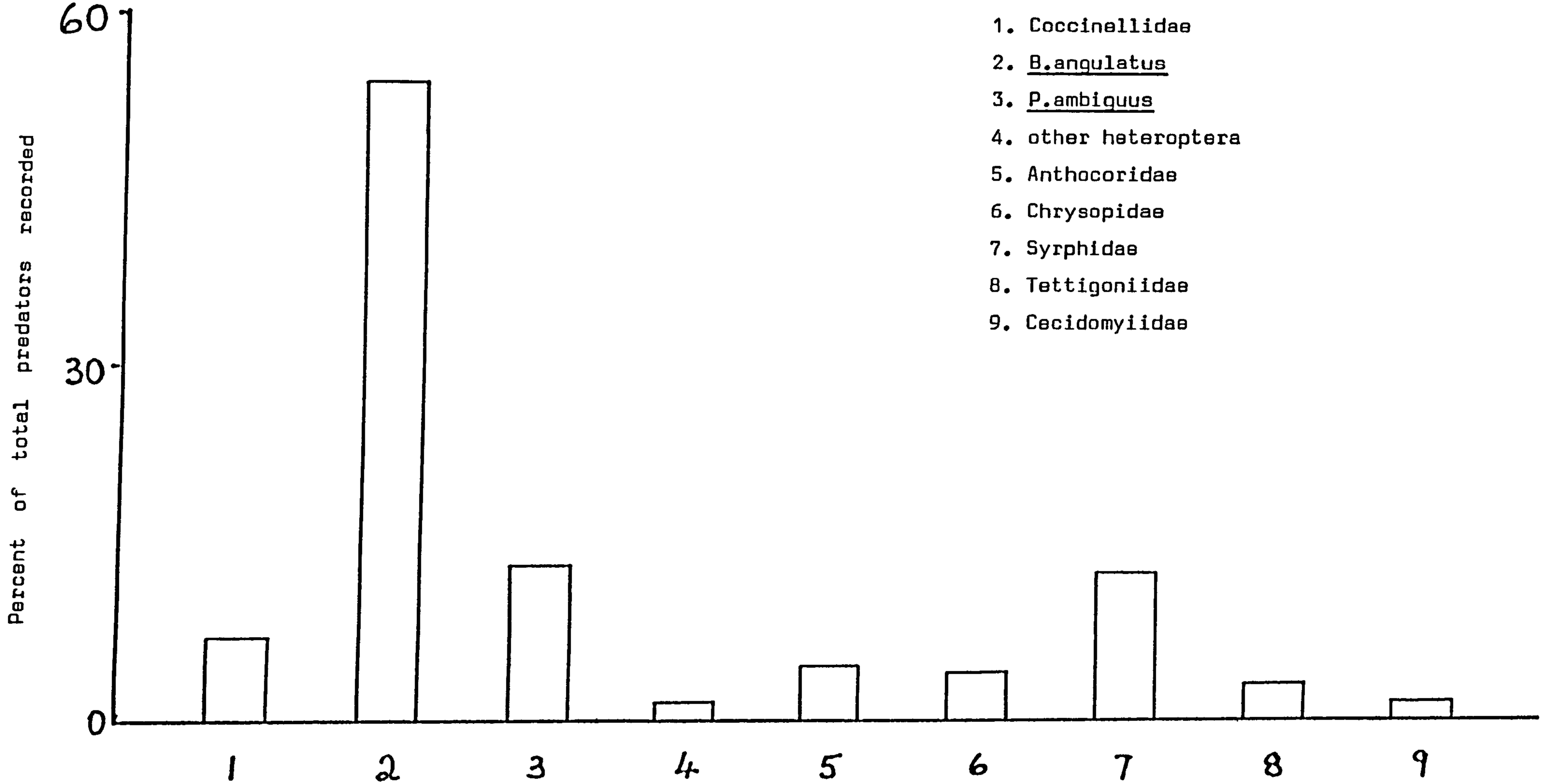


Figure 10: Ratio of predators to aphids during 1982 at Lyne



1. Coccinellidae
2. B.angulatus
3. P.ambiguus
4. other heteroptera
5. Anthocoridae
6. Chrysopidae
7. Syrphidae
8. Tettigoniidae
9. Cecidomyiidae

Figure 11: The relative abundance of predators during 1982 at Lyne.

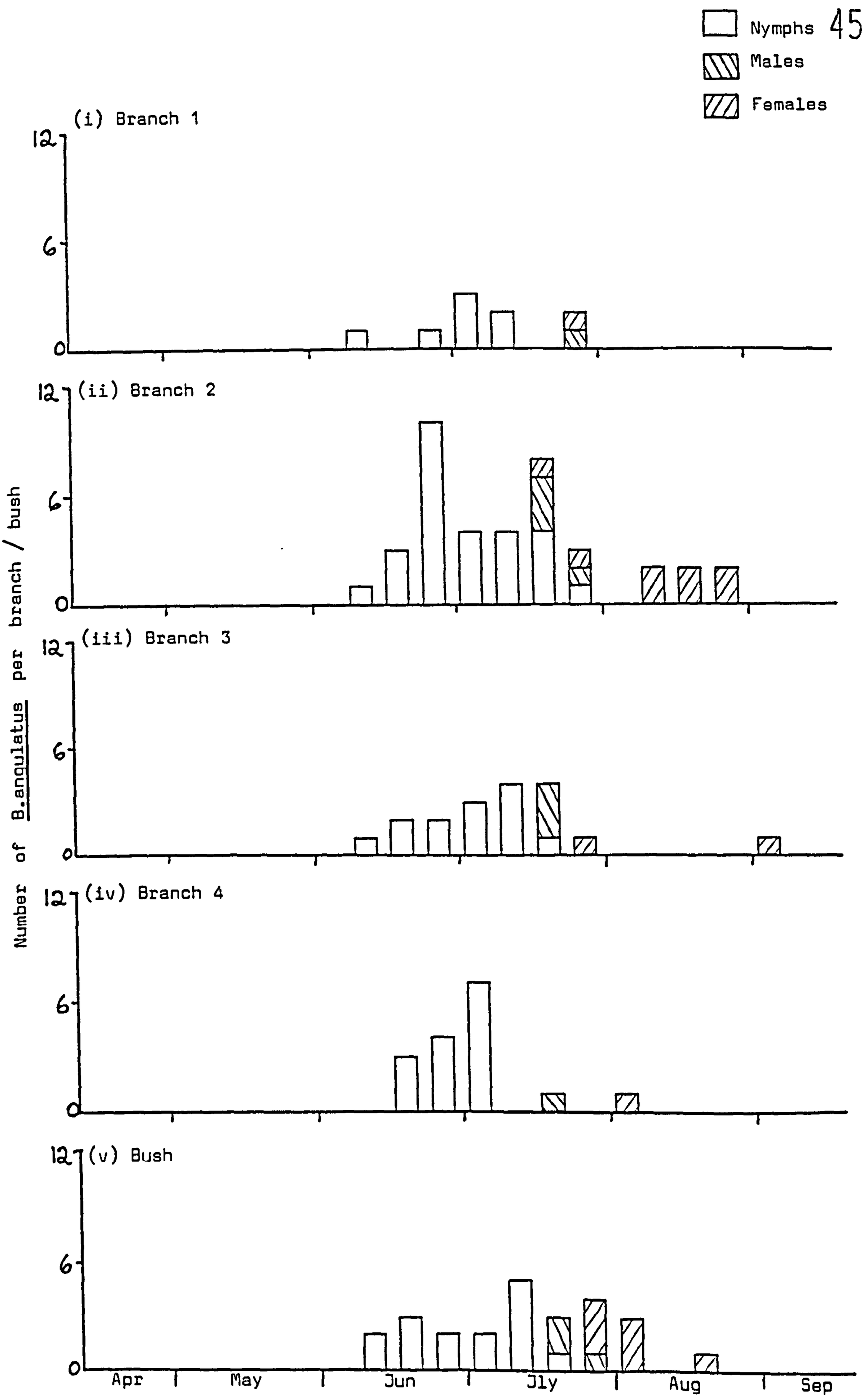


Figure 12: Abundance of B.angulatus during 1982 at Lyne

Larvae of the syrphid fly Metasyrphus luniger Meigen were present from late June until September. The presence of pupae indicated that more than one generation occurred.

The common green lacewing, Chrysoperla carnea Stephens appeared as adults in June and as larvae later in the season. The only other predators recorded were adult specimens of the oak bush cricket, Meconema thalassinum Degeer which appeared in late July and occasional larvae of the cecidomyiid Aphidoletes aphidimyza Rondani.

Parasitism, determined from the number of unemerged mummified aphids present on the branch first manifested itself in early June. It rapidly increased then subsequently remained at relatively low levels until September (fig.13). All mummies taken from non-sample branches produced specimens of Trioxys pallidus Haliday. No incidences of aphids killed by entomopathogenic fungi were recorded.

Occasional adult B.angulatus and A.nemorum were recorded on A.incana and A.cordata but these did not persist, presumably due to the lack of prey.

2.3.2, 1983

(i) Abundance of aphids

Weekly leaf counts are shown in fig.14a,b, c. As in 1982, leaves were shed from early summer onwards and leaf growth had apparently ceased by late June/early July. There were fewer overwintering eggs than during the winter of 1981/82 and fundatrices were only recorded on branches 2,3 and the bush. On branches 1 and 4 the population was initiated by the arrival of alates which appeared in early June. The subsequent populations on all branches rose very rapidly and peaks were reached in mid July (fig.15 a,b,c,d,e,). The patterns of abundance were again similar,

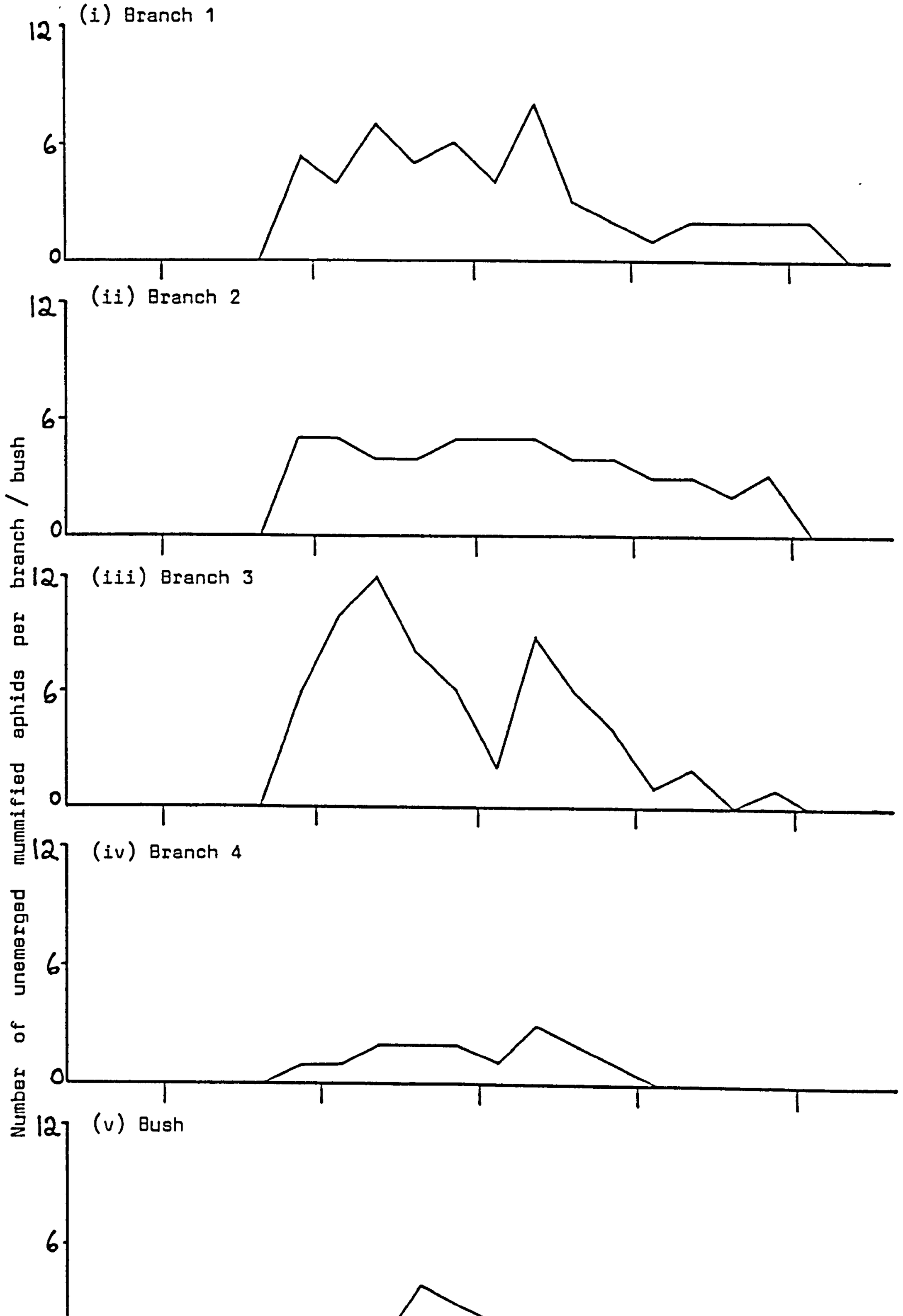


Figure 13: Parasitism in populations of P.alni, Lyne 1982

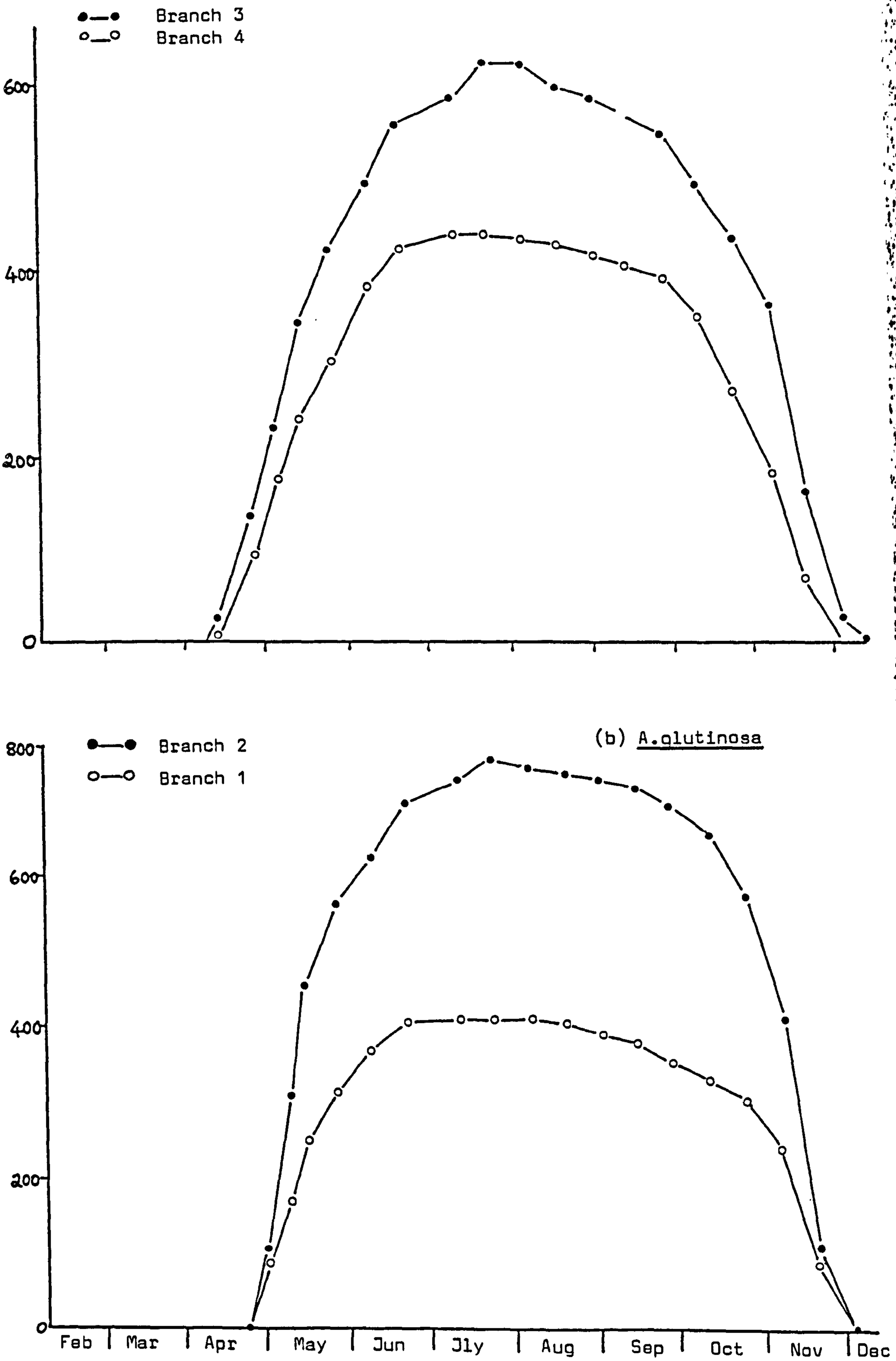


Figure 14: Leaf counts for sampled branches, Lyne 1983

(c) A.glutinosa

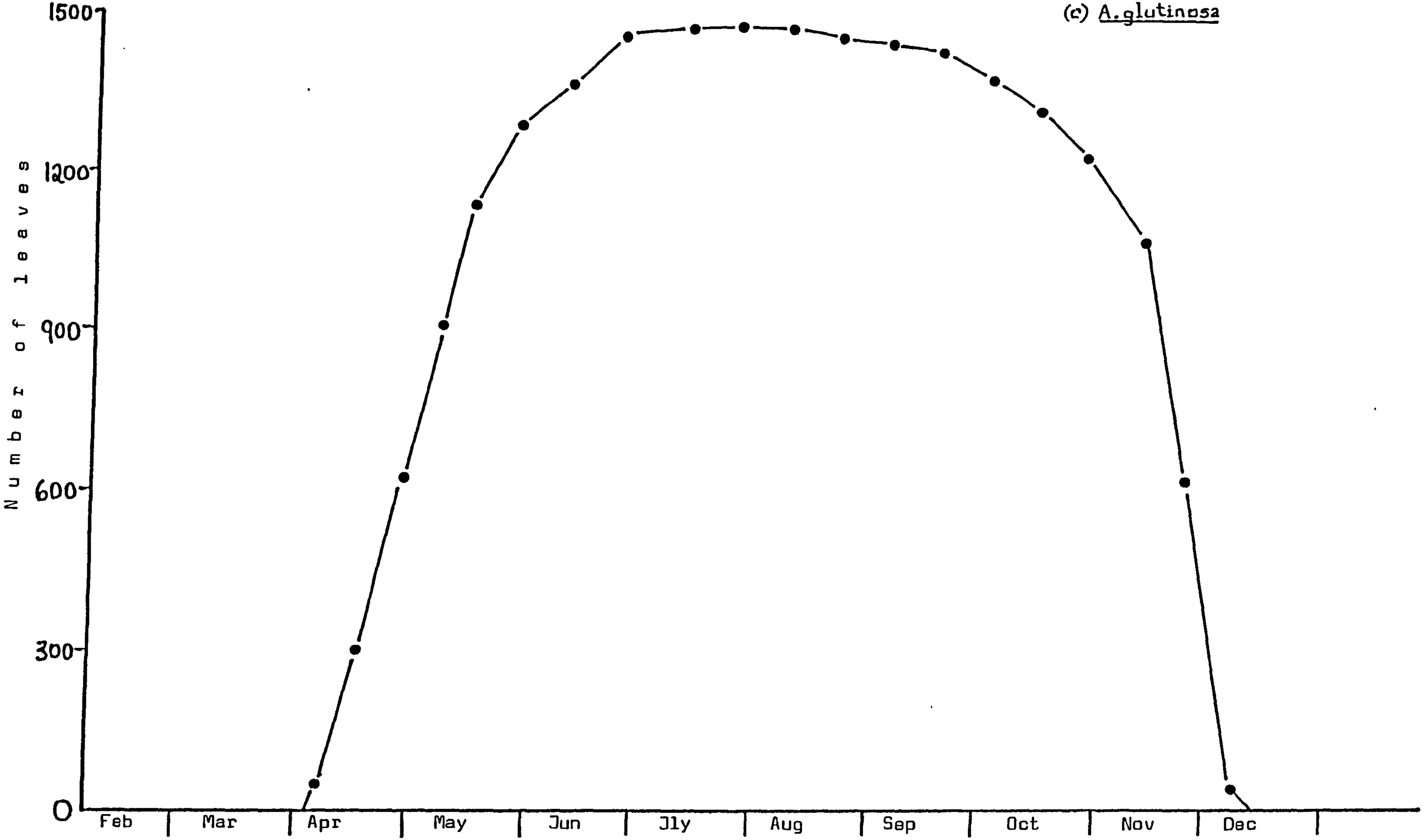


Figure 14: Leaf counts for the bush, Lyne 1983

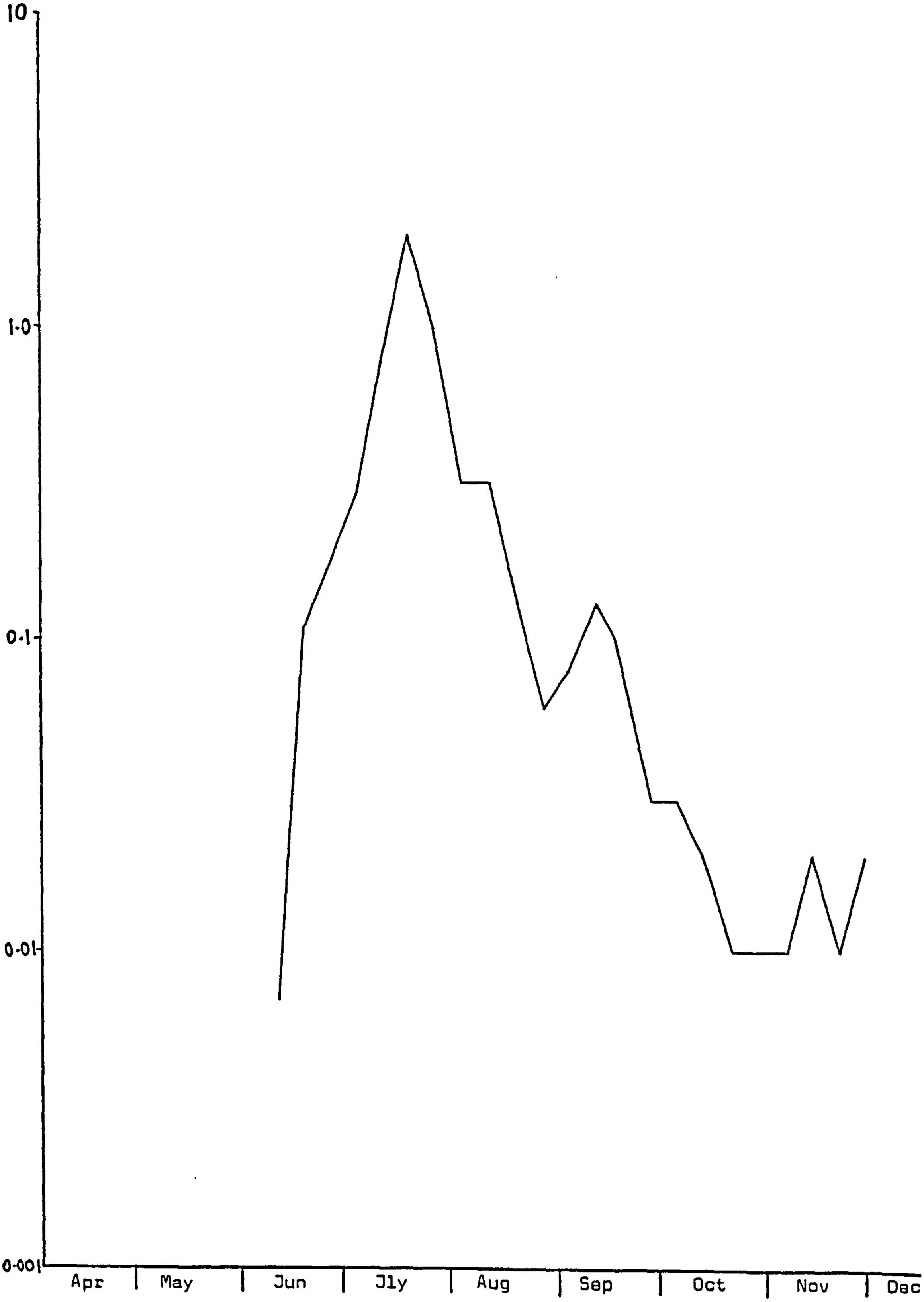


Figure 15 (a): Aphid population, branch 1, Lyne 1983

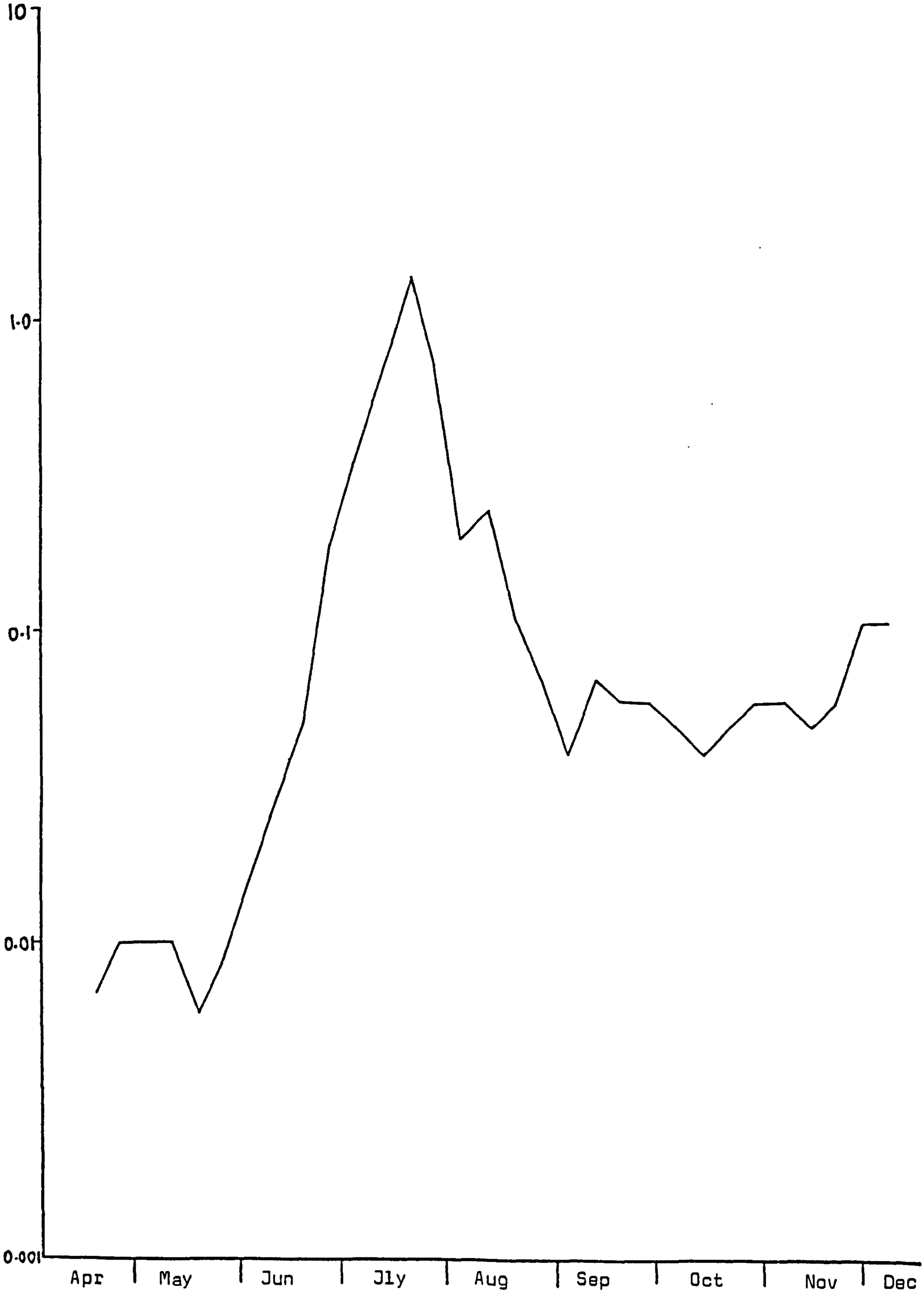


Figure 15 (b): Aphid population, branch 2, Lyne 1983

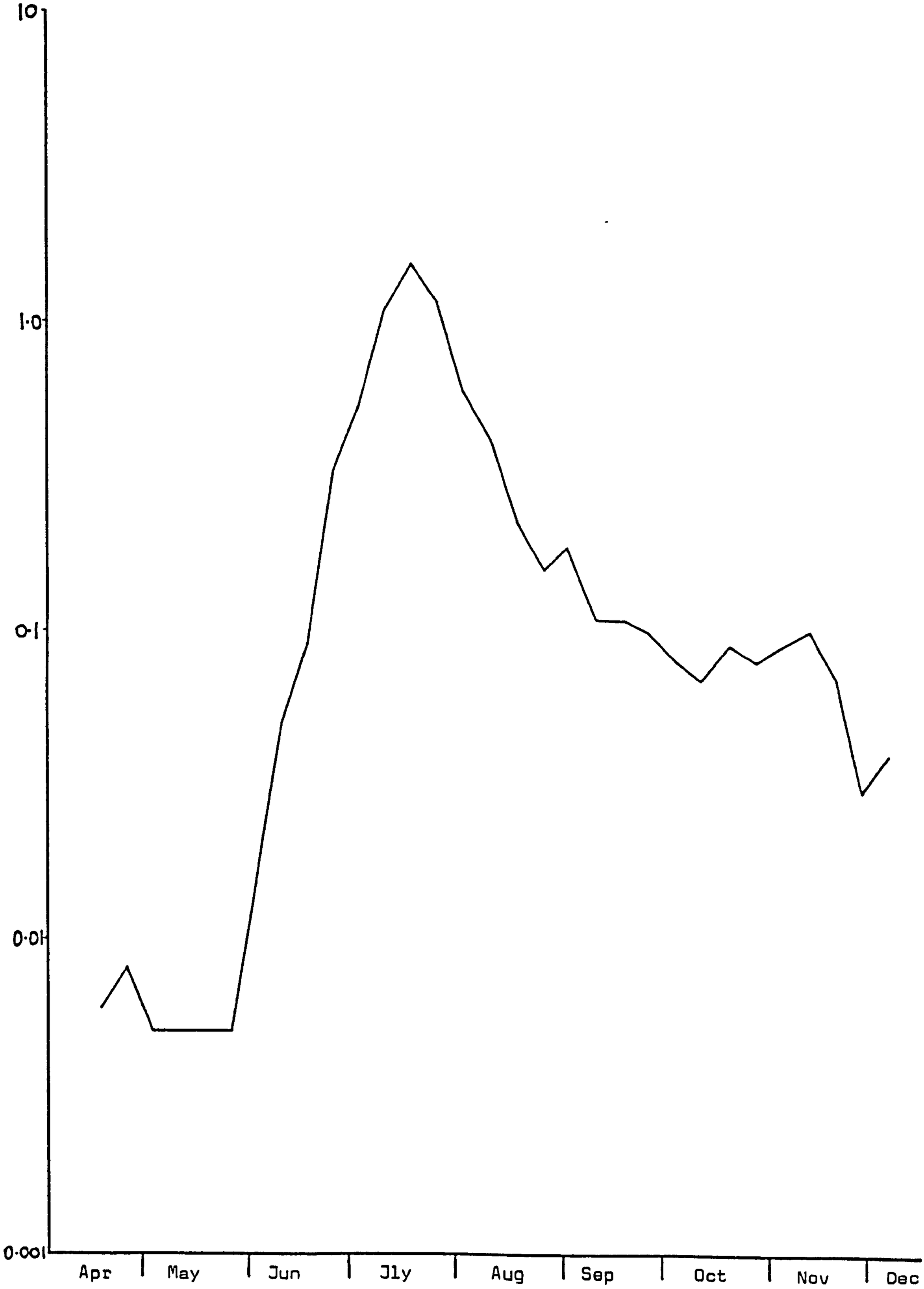


Figure 15 (c): Aphid population, branch 3, Lyne, 1983

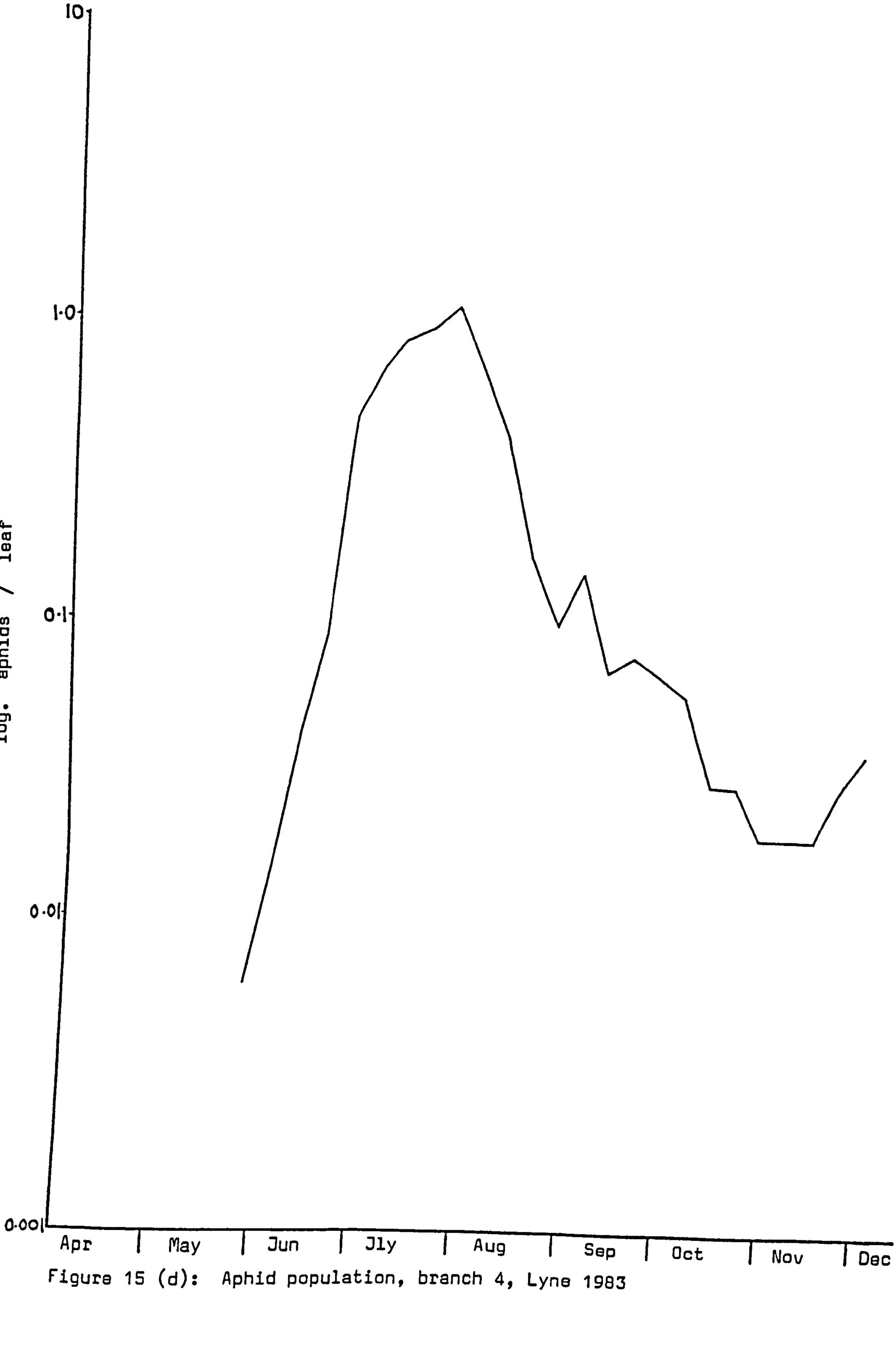


Figure 15 (d): Aphid population, branch 4, Lyne 1983

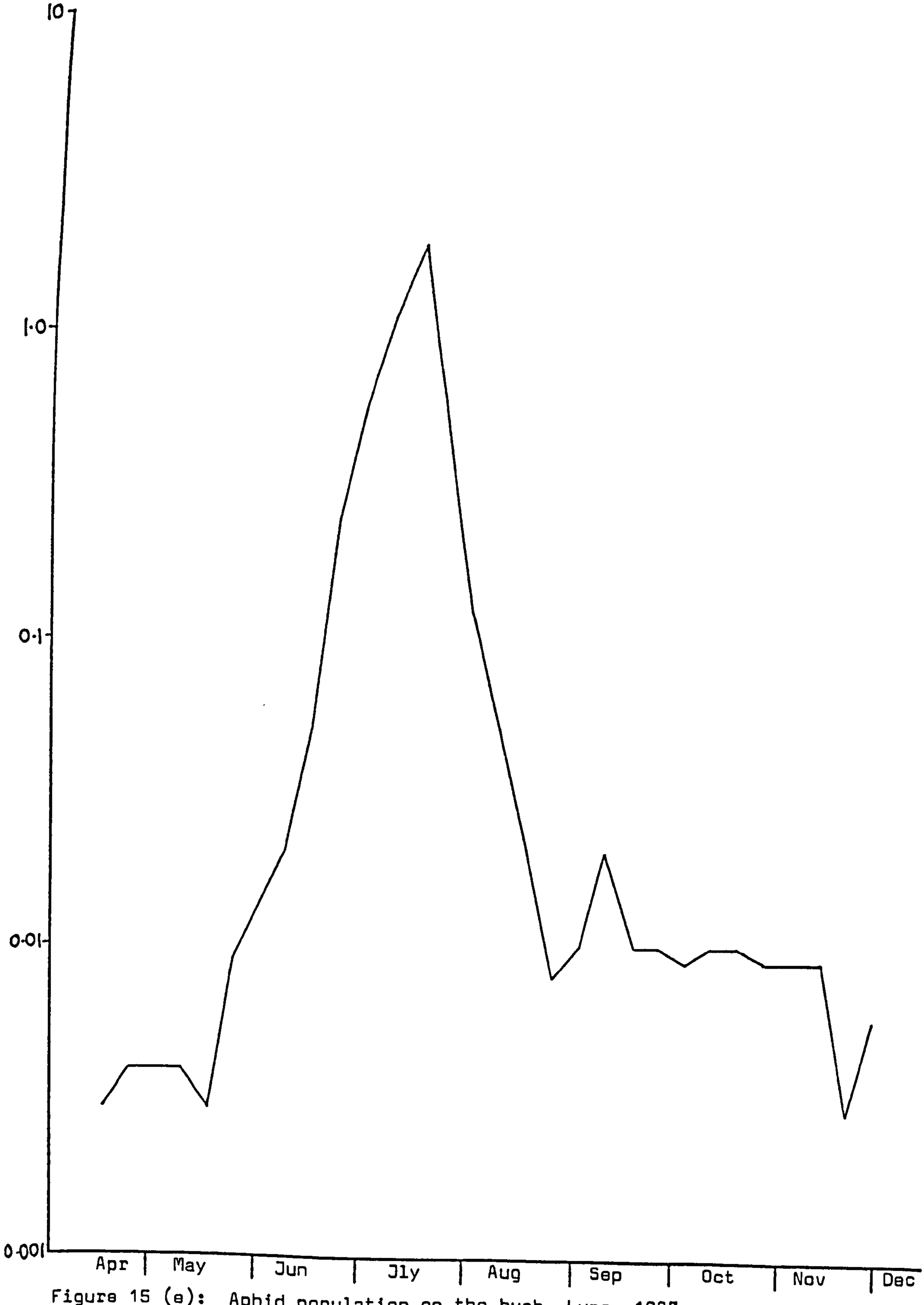


Figure 15 (e): Aphid population on the bush, Lyne, 1983

although total numbers varied (table 4). The decline in numbers was equally rapid. There were resurgences in late August and numbers remained fairly stable until the end of the season. As happened in 1982, only isolated alates appeared on the trees of A.incana and A.cordata . No nymphs were found and no populations were established.

The age structure indicated that throughout the season instars I-III formed over 60% of the population (fig.16 a,b,c,d,e,). Due to the low populations initially there were times when these nymphs were absent on the sampling date and aphids present were fourth instars or adults. During population build up instars I -III generally accounted for 70-80% of the total numbers.

Branches 2,3 and the bush had aphids present on them throughout the season. The histograms of fig.16 b,c and e show that the first generation was apterous, the second mostly so, the third almost entirely alate and the fourth mostly alate. The fifth and sixth generations were apterous. Together with the sexuales in autumn there were seven generations of P.alni at this site in 1983. The alates which arrived on branches 1 and 4 must have been of the second generation at this time of year. These produced nymphs of the third generation which were apterous. The fourth generation here was mostly alate, the fifth mostly apterous and the sixth entirely apterous. Thus of the generations which occurred at this site, the latter five were present on these branches although their morphological composition varied from the other branches sampled.

Fourth instars (presumptive alatae) first appeared in late June. With no significant differences between the proportions, amalgamated data is shown in fig.17. The proportion rose rapidly and on July 13th, 98% of the fourth instar were presumptive alatae. Alatae continued to be produced until mid August.

Table 4 TOTAL APHIDS PER BRANCH - LYNE 1983

Date		Branch 1	Branch 2	Branch 3	Branch 4	Bush
April	20	0	3	2	0	2
	27	0	6	3	0	4
May	4	0	5	2	0	4
	11	0	5	2	0	4
	18	0	3	2	0	3
	25	0	6	2	2	11
June	8	3	17	29	18	25
	15	46	36	57	39	79
	22	75	146	196	209	369
	29	119	273	326	308	849
July	5	324	513	673	386	1596
	13	801	1035	927	412	2732
	20	399	532	689	486	862
	27	129	150	355	294	169
Aug	3	136	185	249	173	75
	10	55	79	135	69	24
	17	23	55	93	40	11
	24	31	30	113	61	13
	31	48	48	63	28	25
Sept	7	34	42	59	33	16
	14	11	39	52	26	14
	21	9	31	39	21	11
	28	8	27	36	10	12
Oct	5	4	31	38	8	12
	12	4	28	33	5	10
	19	3	25	33	3	9
	26	3	14	25	2	7
Nov	2	1	7	11	2	1
	9	1	3	3	1	1
	16	0	1	1	0	0

Figure 16 (a) :

Age structure of the population on branch 1, 1983

(i) Alate adults

(ii) Fourth instars (presumptive alatae)

(iii) Apterous adults

(iv) Fourth instars (presumptive apterae)

(v) Nymphs

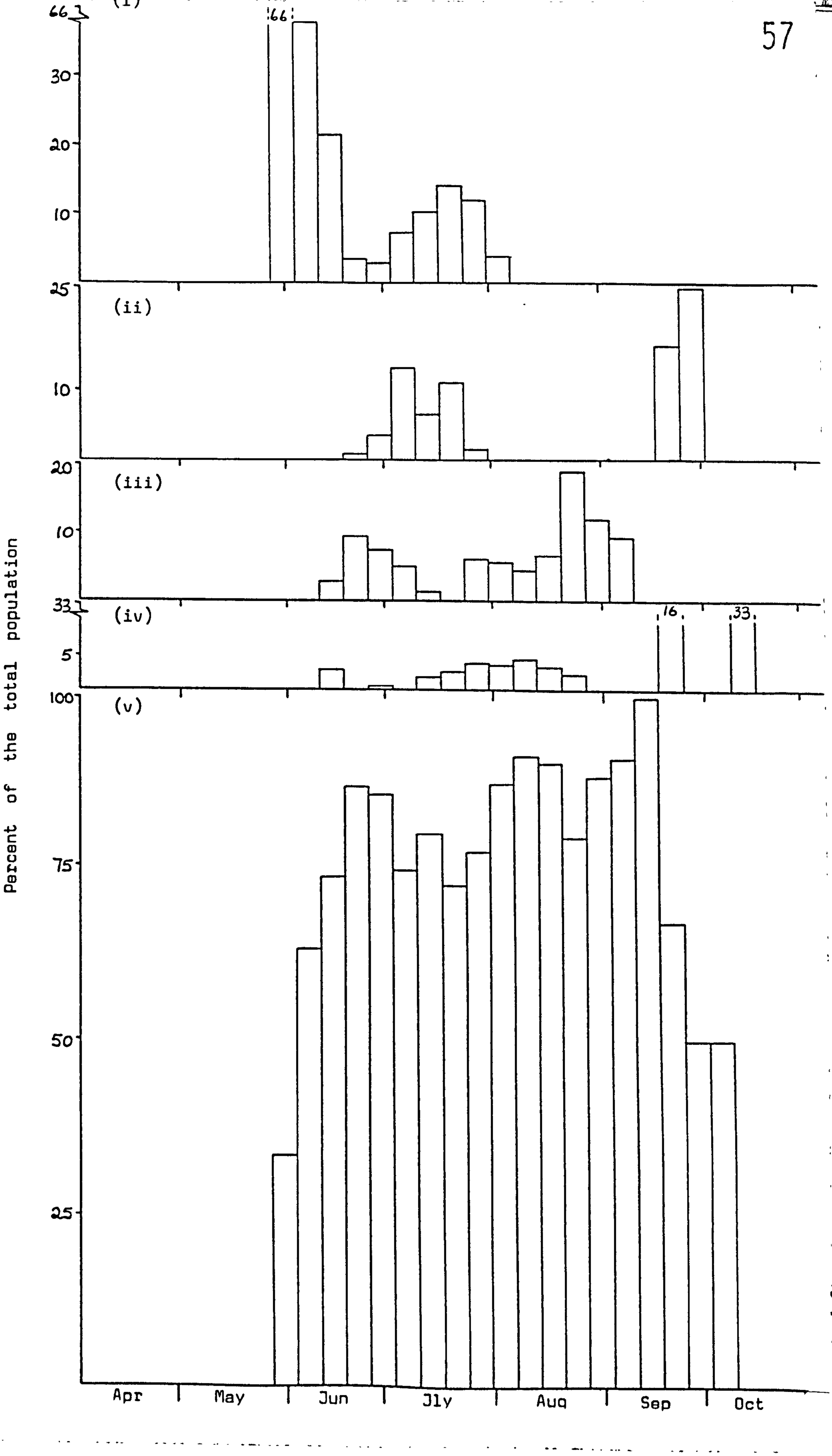

(i)
66
30
20
10
25
(ii)
10
20
(iii)
10
33
(iv)
5
100
(v)
75
50
25
Percent of the total population
66
16
33
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 16 (b) :

Age structure of the population on branch 2, 1983

Legend as for figure 16 (a)

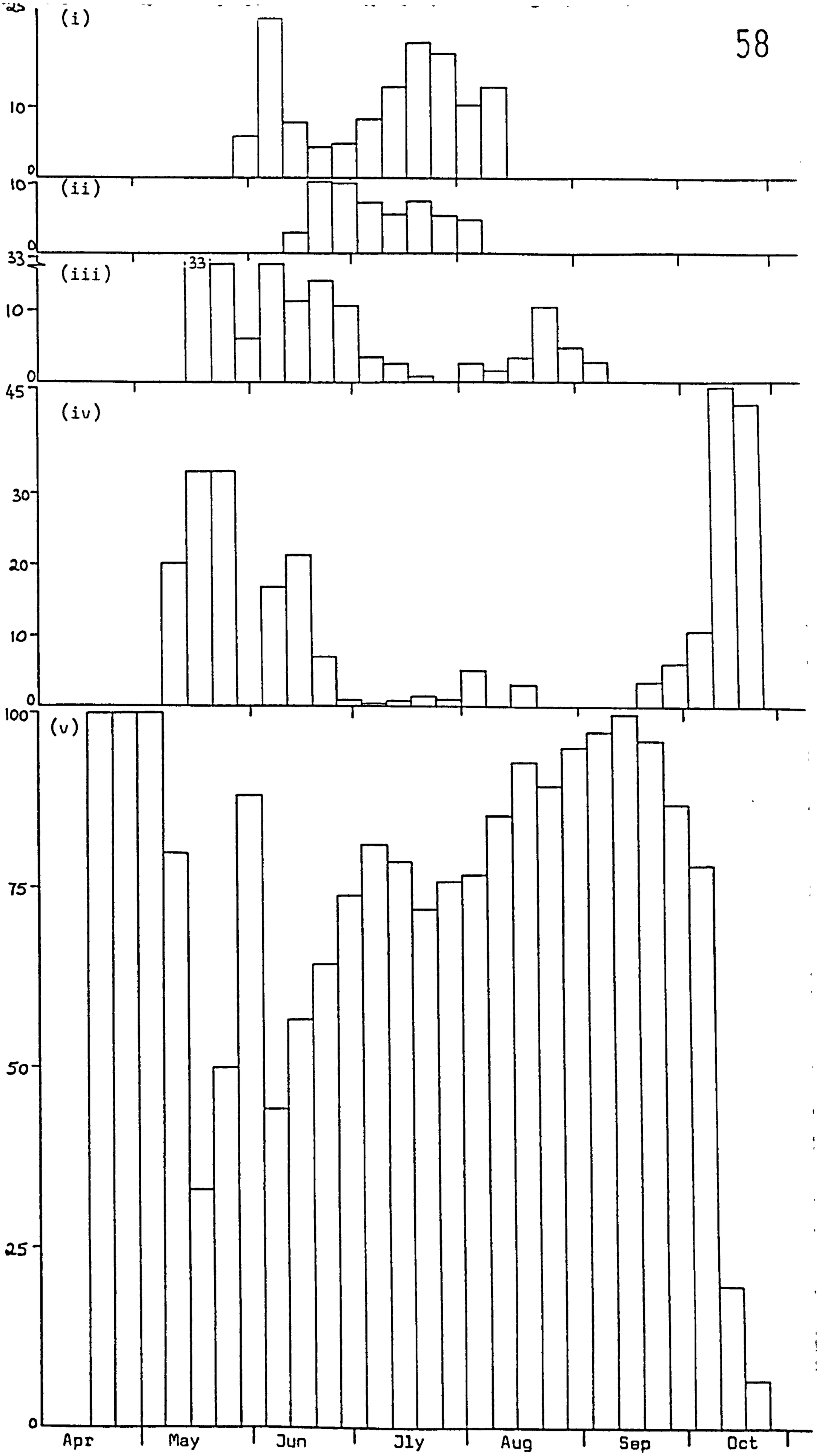

(i)
10
0
(ii)
10
0
33
(iii)
33
10
0
45
(iv)
30
20
10
0
100
(v)
75
50
25
0
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 16 (c) :

Age structure of the population on branch 3, 1983

Legend as for figure 16 (a)

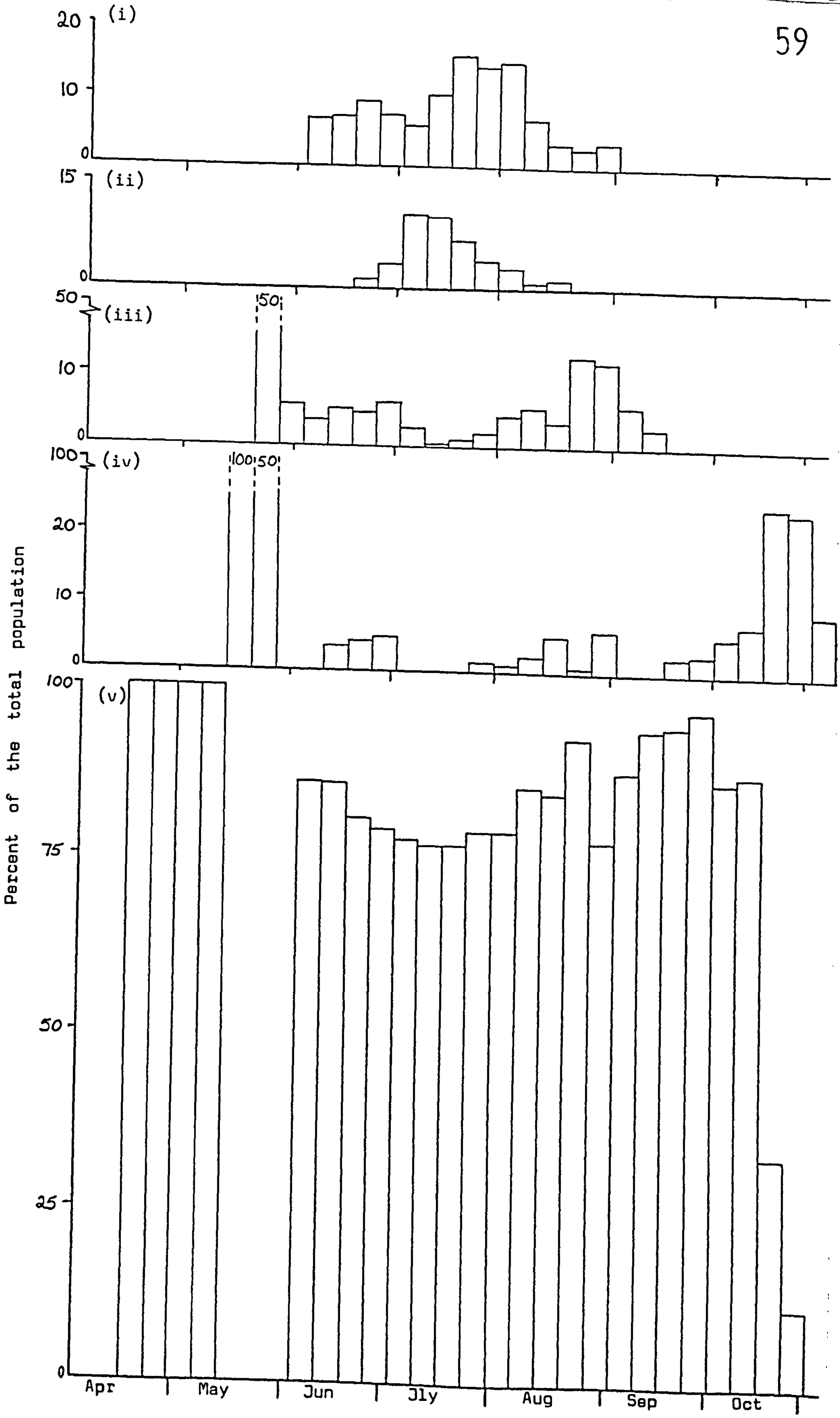

(i)
20
10
0
(ii)
15
0
(iii)
50
150
10
0
(iv)
100
100
50
20
10
0
(v)
100
Percent of the total population
75
50
25
0
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 16 (d) :

Age structure of the population on branch 4, 1983

Legend as for figure 16 (a)

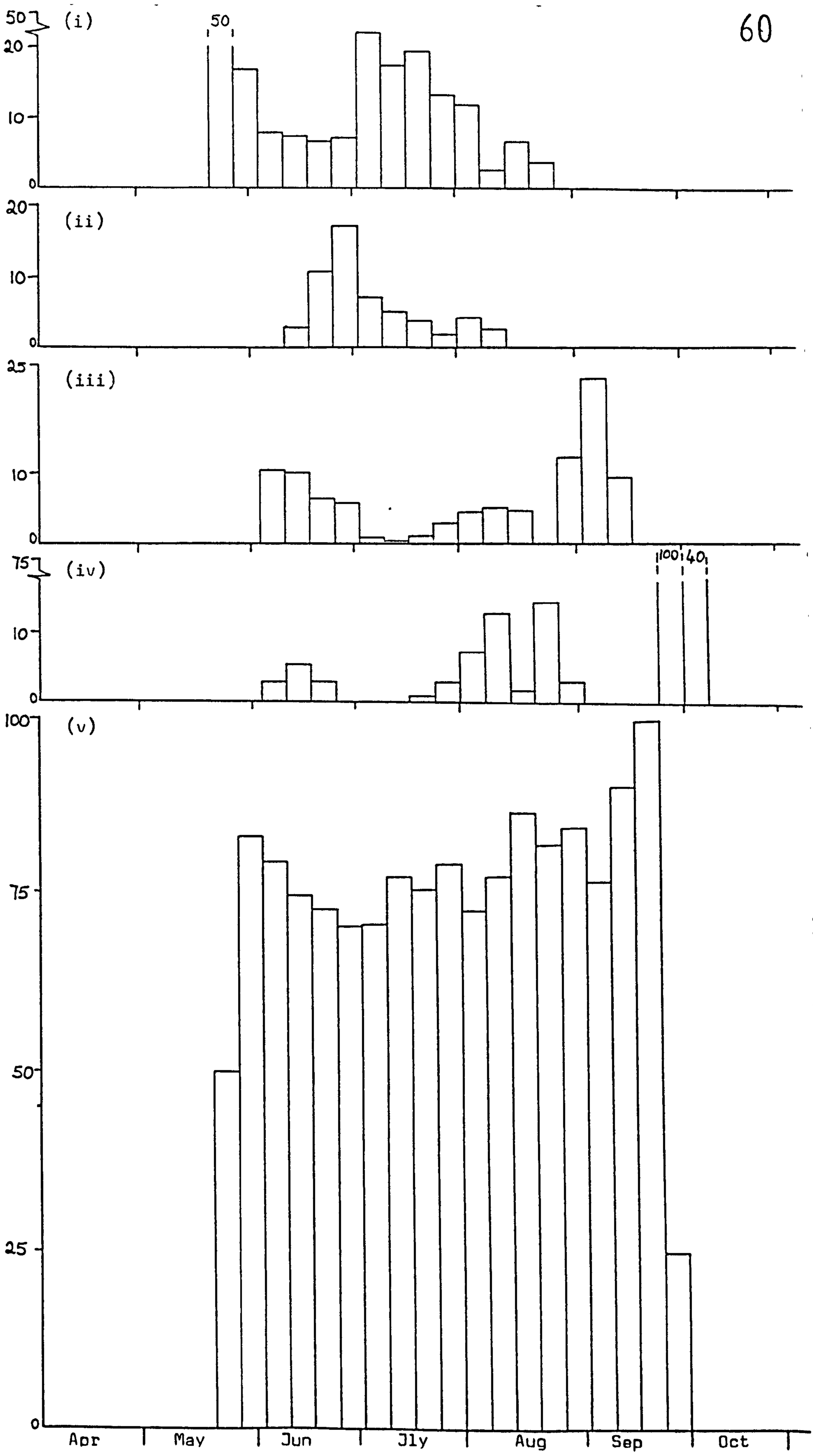
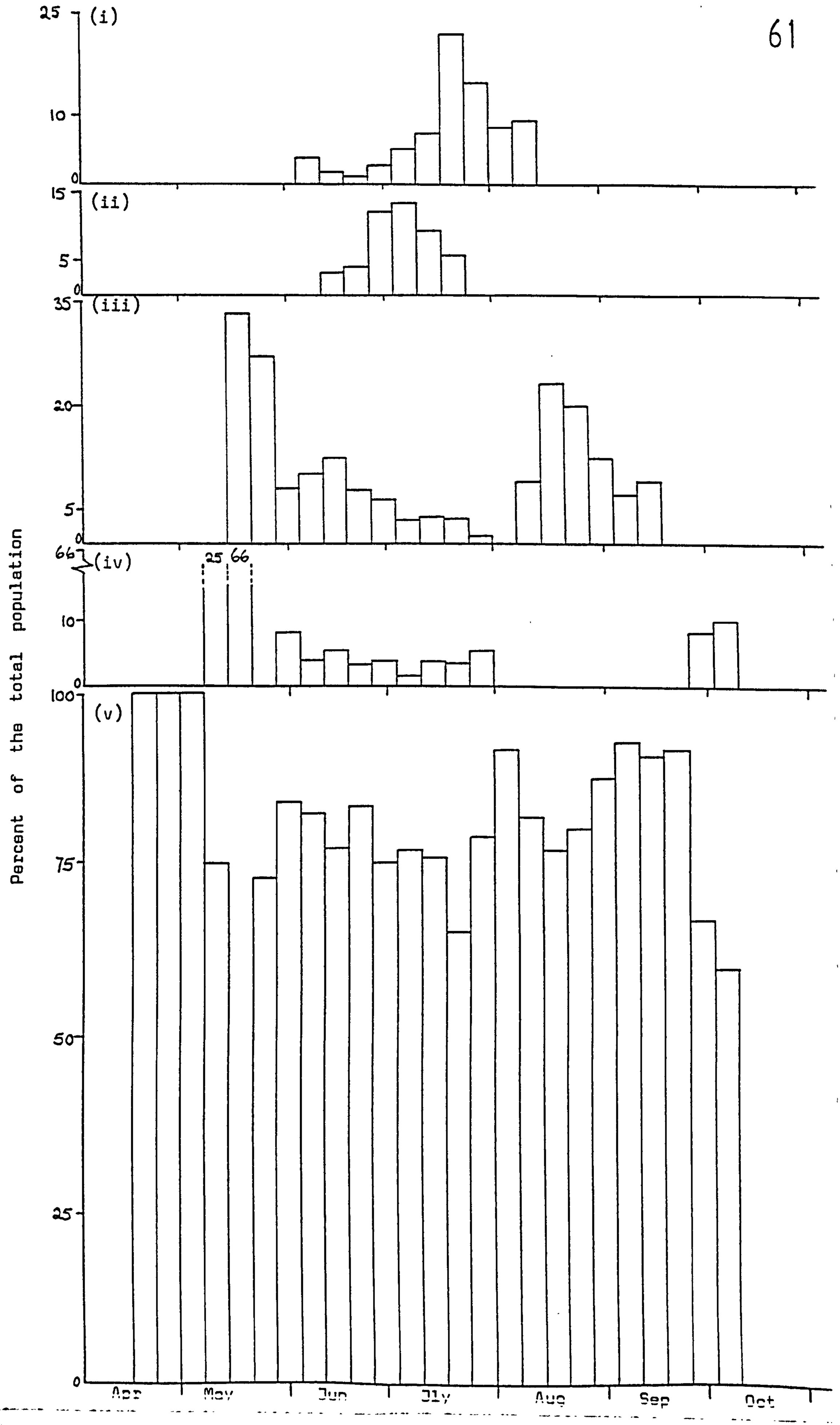

(i)
50
50
20
10
0
(ii)
20
10
0
(iii)
25
10
0
(iv)
75
10
0
100
40
(v)
100
75
50
25
0
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 16 (e):

Age structure of the population on the bush, 1983

Legend as for figure 16 (a)


(i)
25
10
0
(ii)
15
5
0
(iii)
35
20
5
0
(iv)
66
25
66
10
0
(v)
100
75
50
25
0
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct

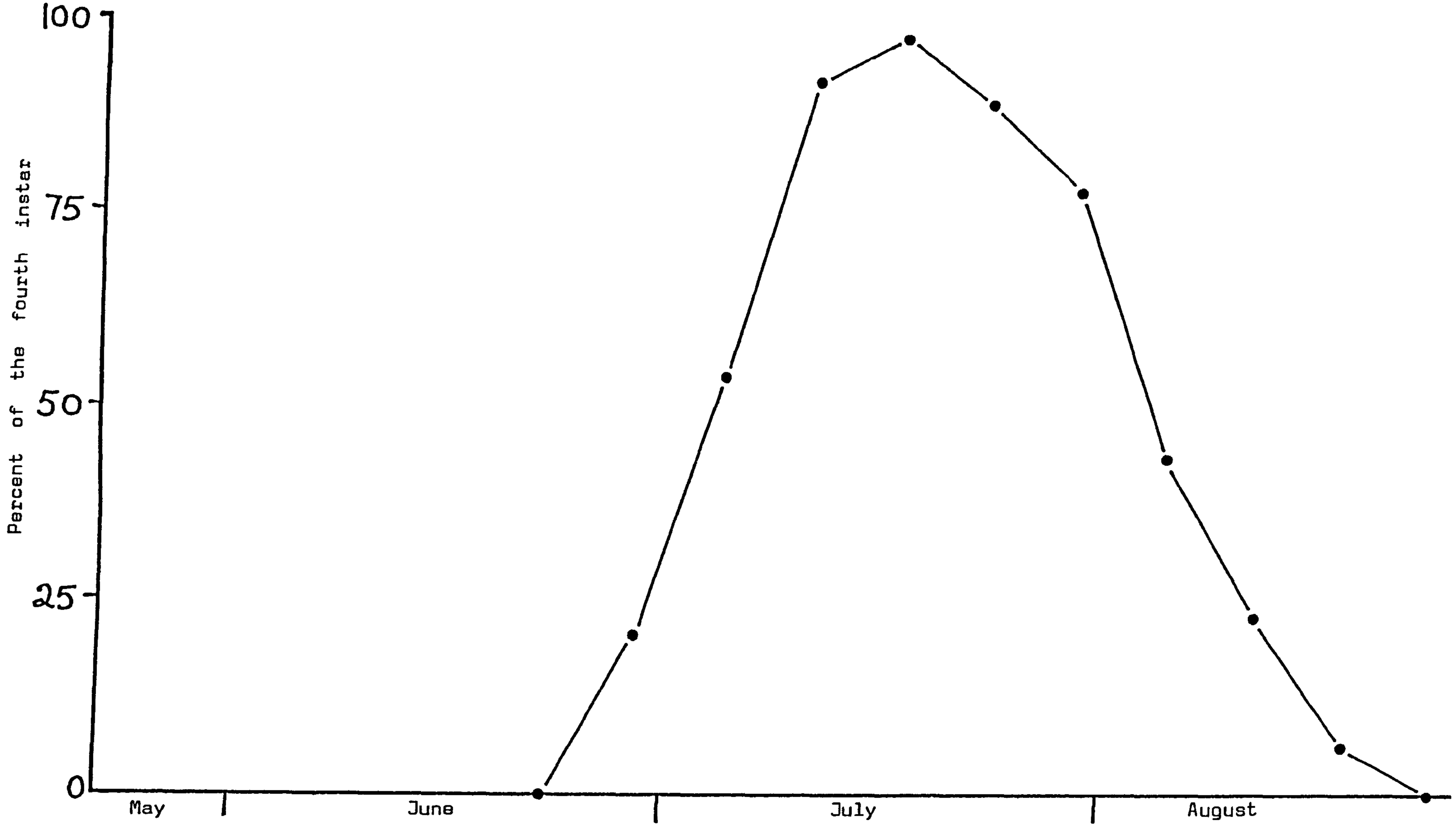


Figure 17: Proportion of presumptive alatae in the fourth instar, all branches, June 1983

Sexual forms appeared from late September onwards (fig.18). Males were fewer in number than the oviparae which occurred from early October until late November (fig.19).

(ii) Spatial distribution of aphids

The value of b in Taylor's power law was significantly greater than one for the bush and all branches for the season, indicating that the aphids were aggregated (table 2). When the population was low the variance was less than or equal to the mean indicating that the dispersion was regular. This was confirmed by the value of zero for Morisita's index at the beginning and end of the season (table 5). The value of the index rose early in the season when the first generation began reproducing. It stabilized at a relatively low level during population build up then increased when the low numbers of the late summer generations began reproducing. Finally it became zero when the low autumnal numbers were distributed as one per leaf (appendix 1.4,1.5,1.6).

(iii) Abundance of natural enemies

Total predator numbers are shown in fig.20 and the ratio of predators to aphids in fig.21. The first predators to arrive in the spring were coccinellids and anthocorids. A.bipunctata appeared in late May and larvae were found later. Coccinella septempunctata L. was also recorded occasionally during the year. A.nemorum adults arrived in early June and were recorded on occasions throughout the summer. P.ambiguus also appeared in early June and the adults persisted until late July. The commonest predator was again B.angulatus accounting for 67% of the total numbers recorded (fig.22). Nymphs of this bug appeared in late June and adults in late July. A rapid decline again occurred, but females persisted well into September (fig.23). C.carnea adults appeared in late May and larvae were found throughout the summer. Larvae of M.luniger were again recorded

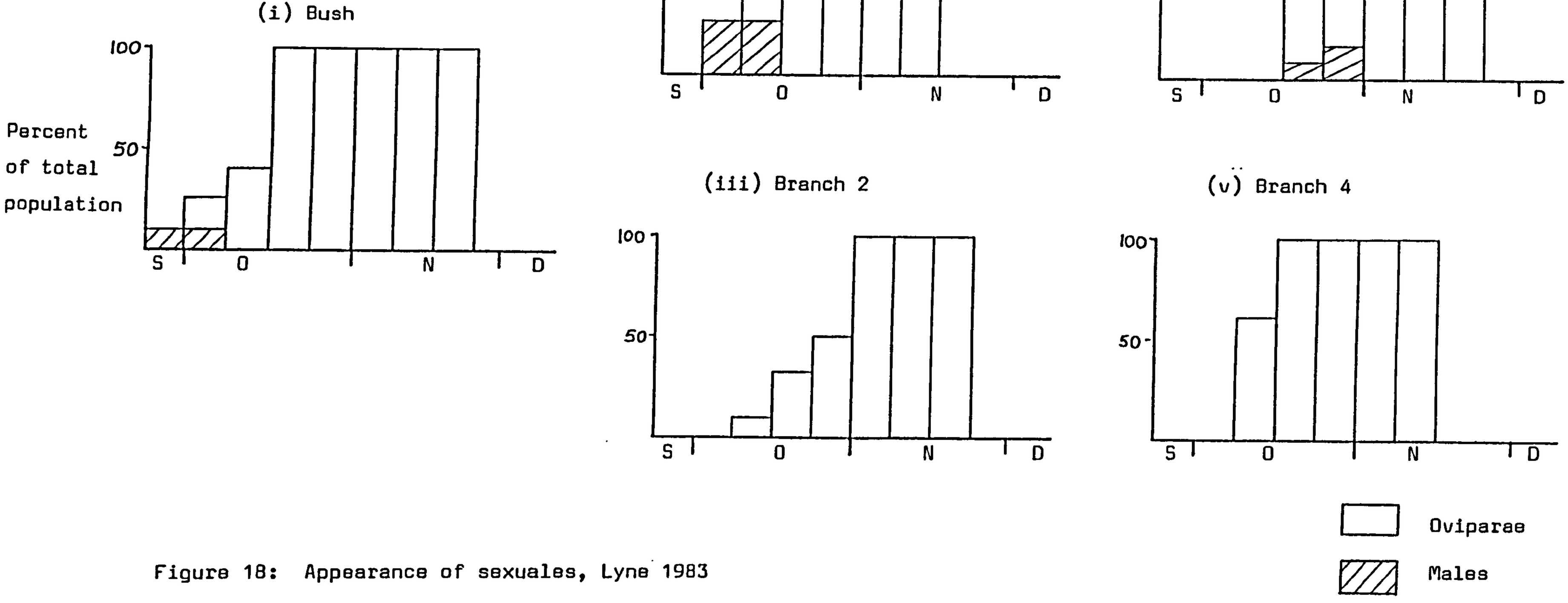
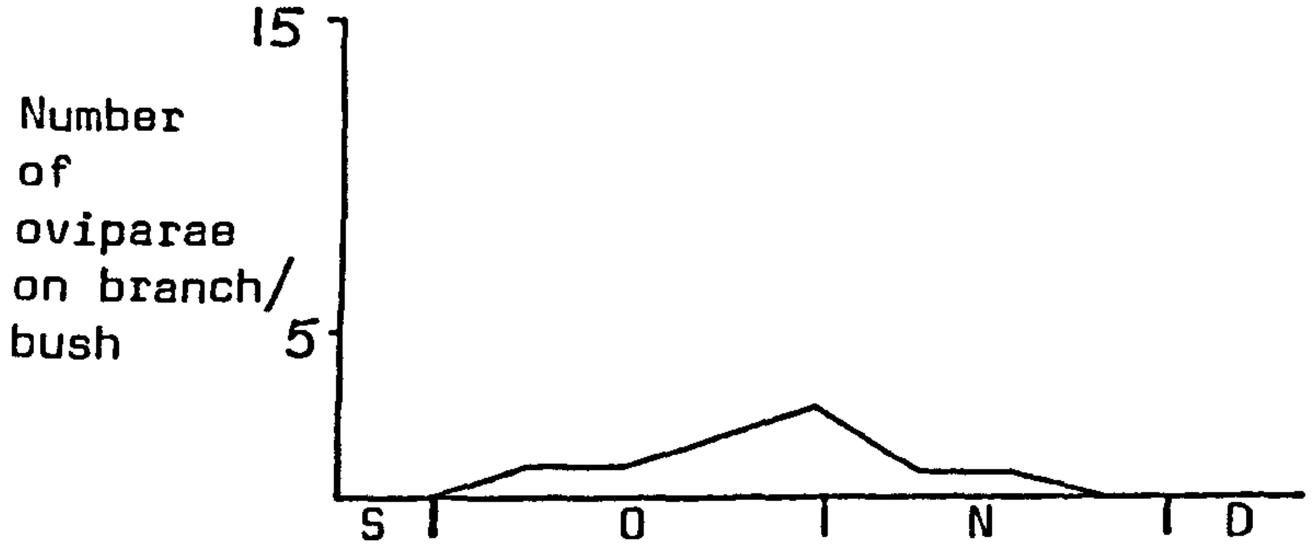
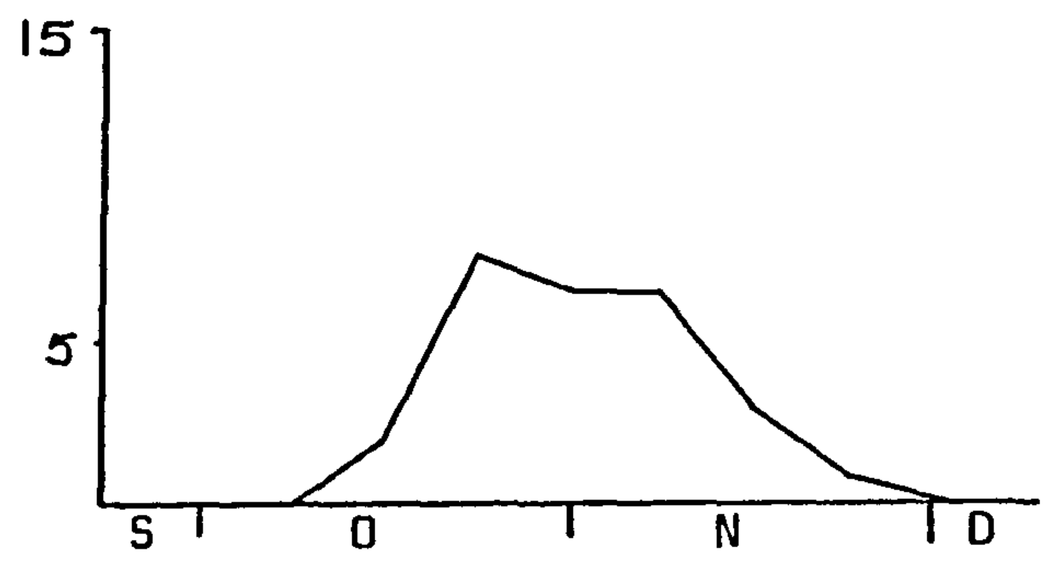
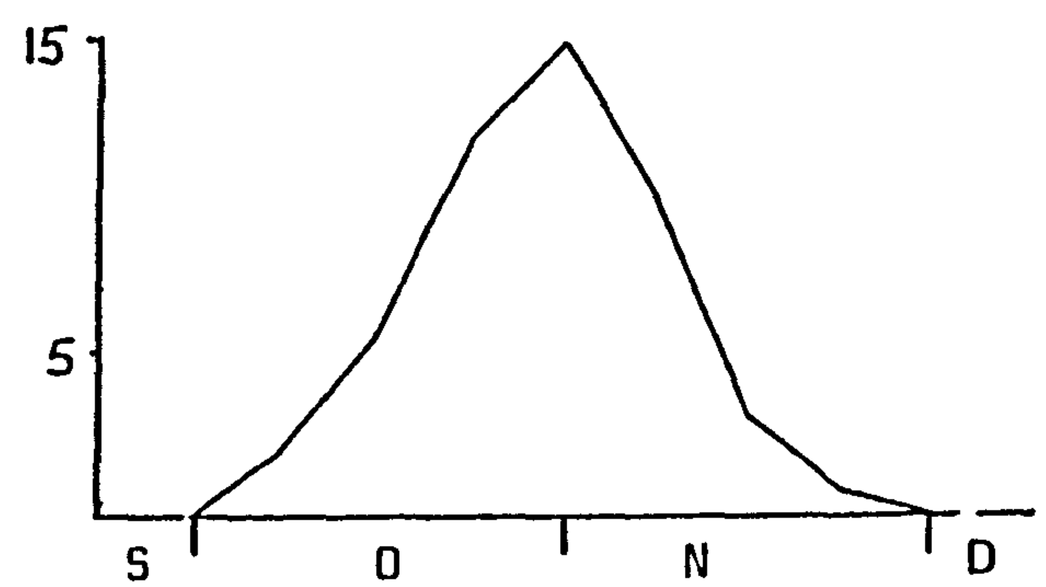
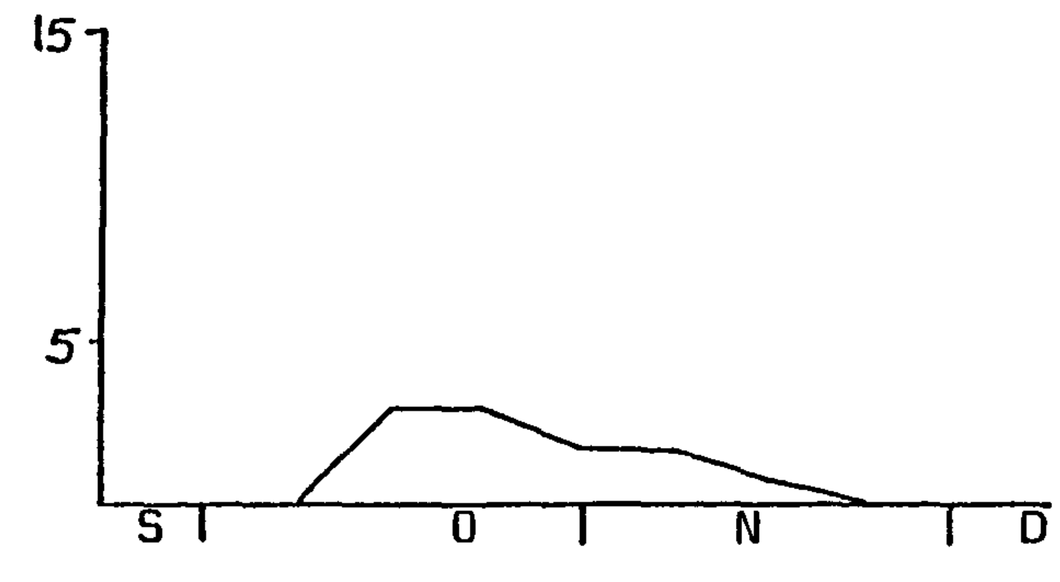


Figure 18: Appearance of sexuales, Lyne 1983









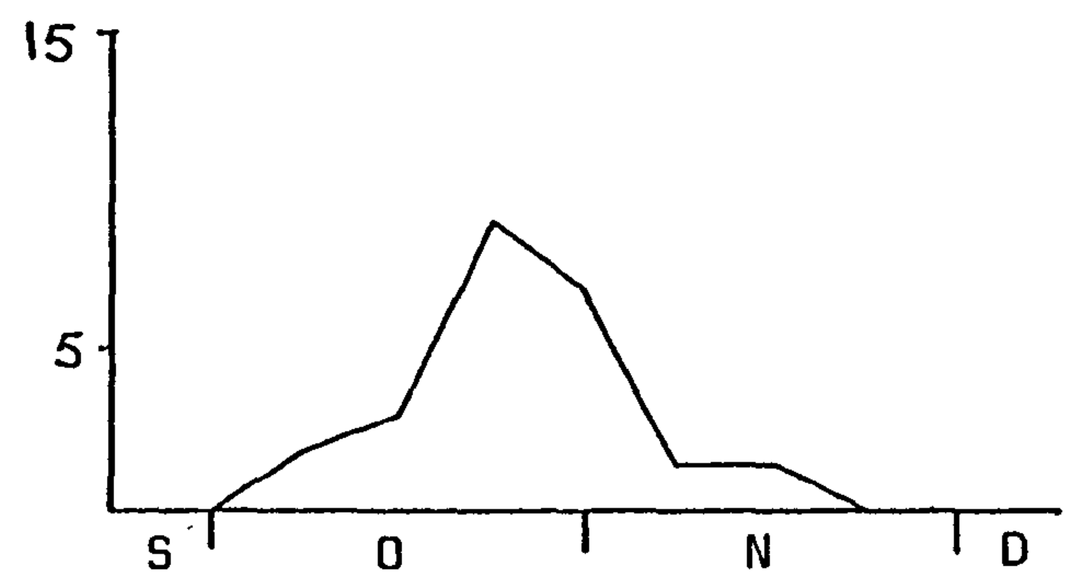


Figure 19: Numbers of oviparae, Lyne 1983

Table 5 MORISITA'S INDEX OF DISPERSION, LYNE 1983

Date		Branch 1	Branch 2	Branch 3	Branch 4	Bush
April	20	0.0	0.0	0.0	0.0	0.0
	27	0.0	0.0	0.0	0.0	0.0
May	4	0.0	0.0	0.0	0.0	0.0
	11	0.0	0.0	0.0	0.0	0.0
	18	0.0	0.0	0.0	0.0	0.0
	25	0.0	278.4	0.0	420.0	530.9
June	8	135.0	95.2	201.1	72.8	230.4
	15	69.6	46.5	68.9	11.7	413.5
	22	48.1	23.6	9.4	15.3	91.6
	29	47.1	19.3	9.9	17.7	15.6
July	5	44.9	18.2	8.9	8.1	10.2
	13	4.4	5.2	5.0	6.5	6.1
	20	5.1	7.1	6.4	5.1	11.9
	27	4.9	6.4	7.3	4.2	14.3
Aug	3	4.5	5.2	4.9	7.5	27.3
	10	5.8	8.7	4.7	7.5	15.7
	17	6.2	14.0	8.3	7.9	104.7
	24	32.0	4.9	10.6	7.1	73.5
	31	11.4	18.7	17.2	23.8	65.6
Sept	7	17.5	31.7	19.2	18.5	57.4
	14	25.1	24.8	17.5	11.1	44.6
	21	9.2	15.4	14.2	9.2	35.9
	28	0.0	13.3	15.2	7.0	29.3
Oct	5	0.0	11.1	15.0	0.0	28.1
	12	0.0	7.3	7.0	0.0	0.0
	19	0.0	5.5	12.7	0.0	0.0
	26	0.0	0.0	6.5	0.0	0.0
Nov	2	0.0	0.0	6.0	0.0	0.0
	9	0.0	0.0	0.0	0.0	0.0
	16	0.0	0.0	0.0	0.0	0.0

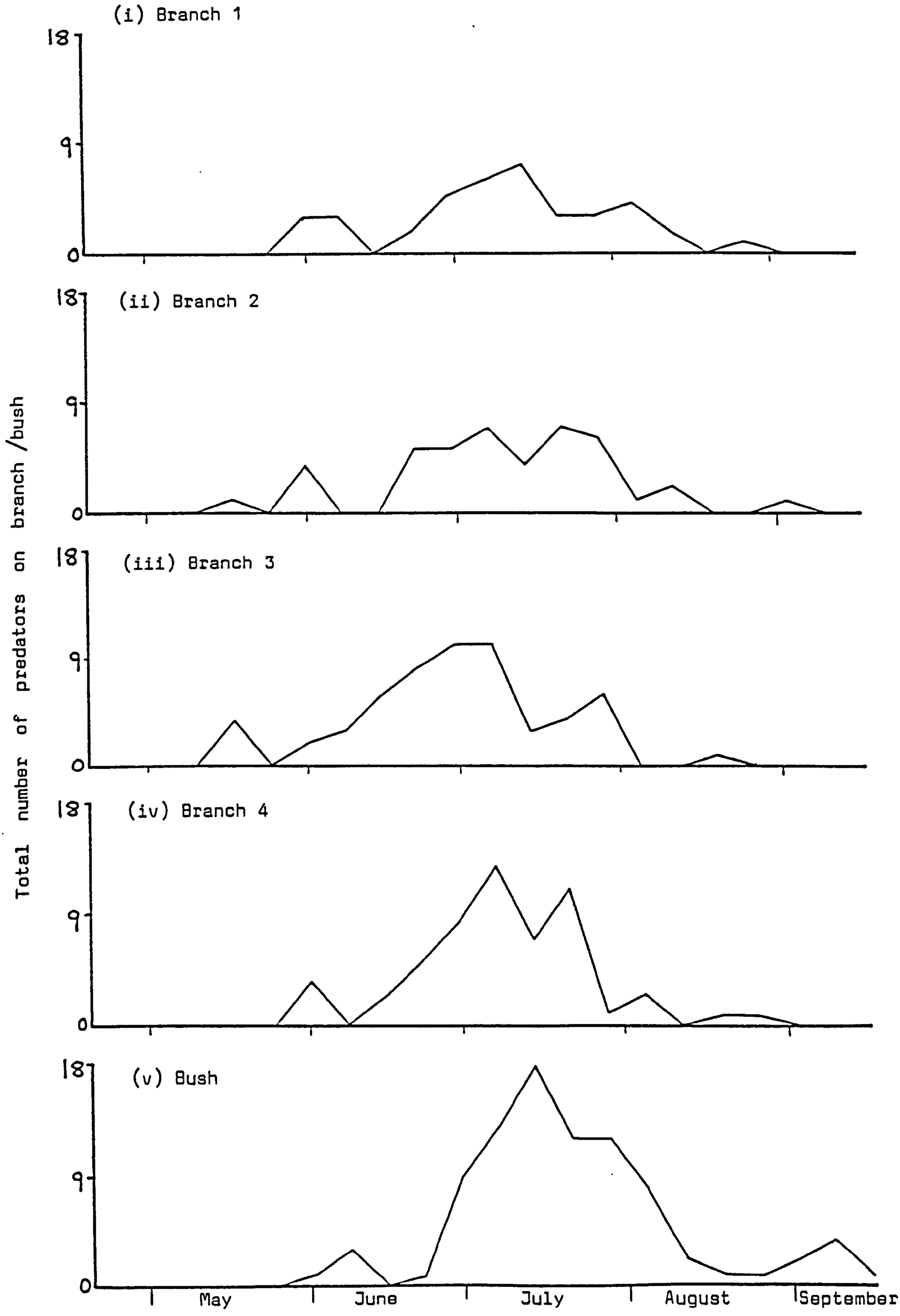


Figure 20: Total numbers of predators during 1983 at Lyne

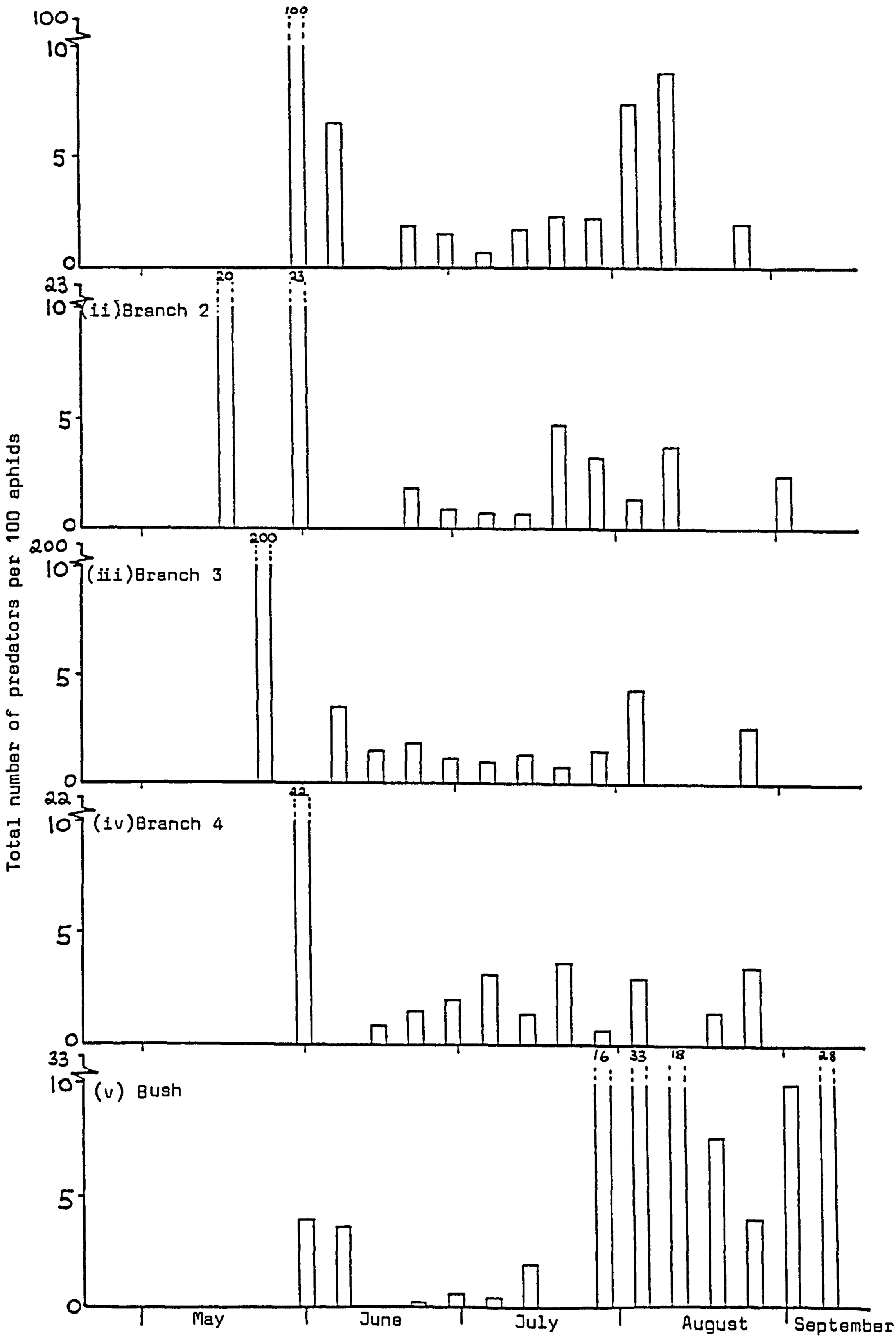


Figure 21: Ratio of predators to aphids during 1983 at Lyne

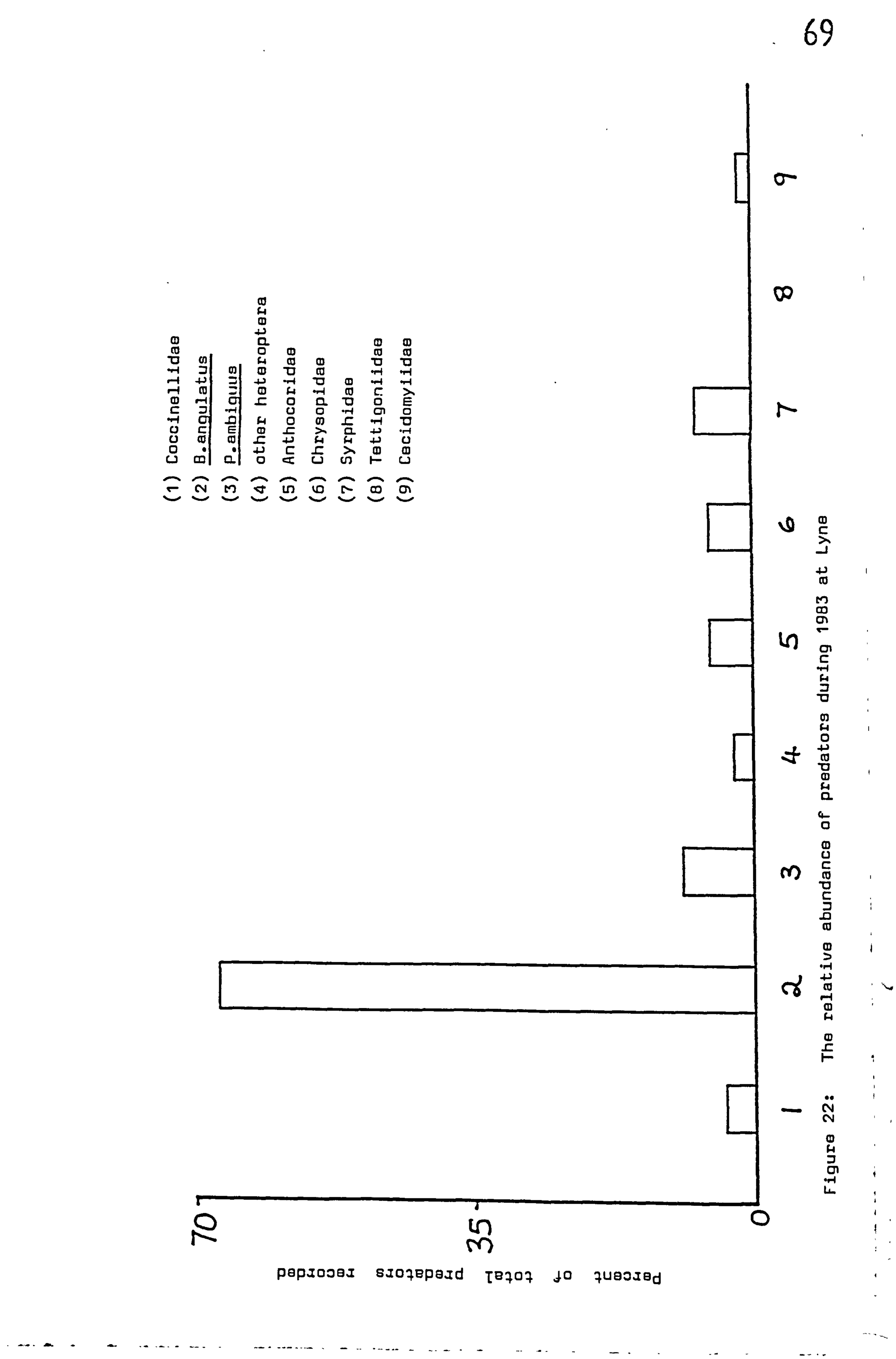


Figure 22: The relative abundance of predators during 1983 at Lyna

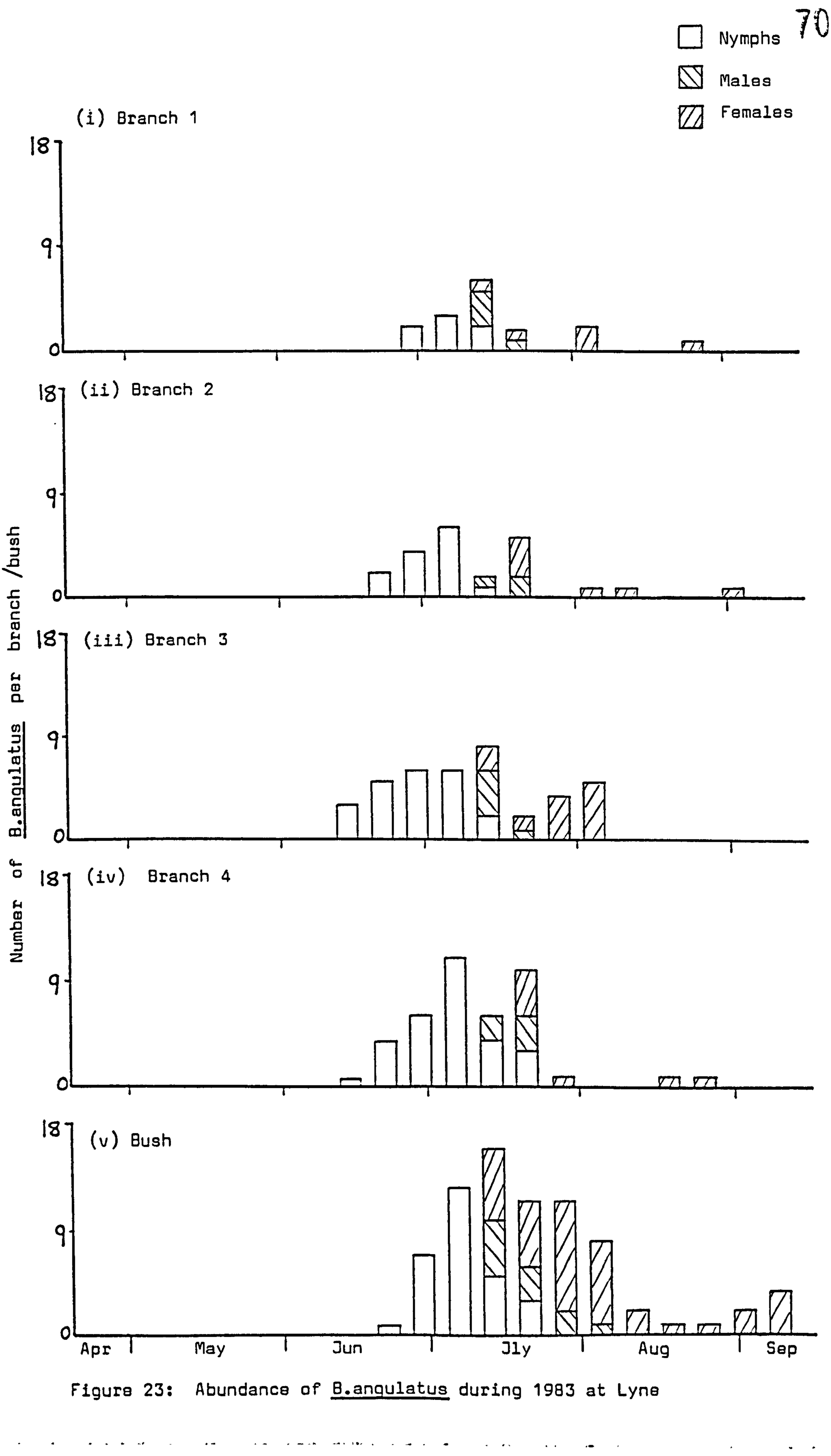


Figure 23: Abundance of B.angulatus during 1983 at Lyne

during July. P.rufipes was found occasionally and larvae of A.aphidimyza were again rare. Parasitism by T.pallidus first became apparent in late June and mummified aphids were found throughout the summer until early October (fig.24). No incidence of death from fungal attack was recorded.

B.angulatus adults were the only predators found on A.incana and A.cordata These appeared in very small numbers (never more than two per two hundred leaf sample) in early August. They soon disappeared due to the lack of available prey as in 1982.

(iv) Meteorological data

Temperatures were plotted as twice weekly means and are given in fig.25. Temperatures in 1983 were lower than 1982 during most of April, May and the early part of June. During July, August and September 1983 temperatures were generally warmer than in 1982 by about 4 - 5^{o}C. The autumn of 1983 experienced lower temperatures than 1982. Frosts (minimum temperature -5.0^{o}C) were recorded in early November 1983 whereas none occurred until the last days of the month in 1982.

2.3.3. The between-year population dynamics

The population graphs summarized in fig.26 show that within a year the changes in aphid populations on the bush and four branches sampled were very similar. However, between the years they were strikingly different. The population peaks were reached earlier in the season in 1982 and in all cases the numbers attained were less than the corresponding totals for the same branches in 1983. In all cases there were considerably more fundatrices present in April 1982 than April 1983. The relative growth rates of the populations also differed considerably (table 6). It is likely that these differences reflect the warmer temperatures experienced

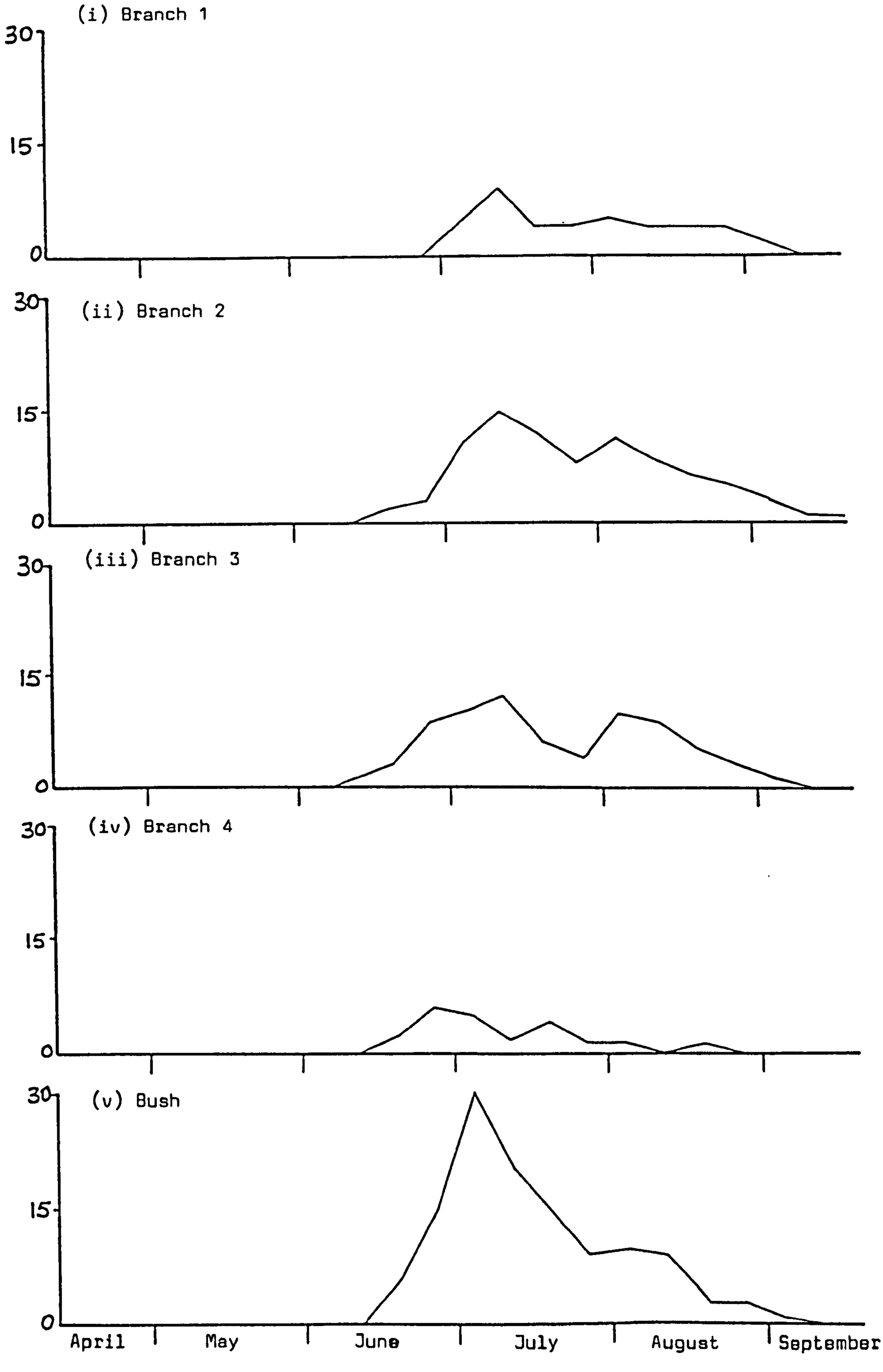


Figure 24: Parasitism in populations of P.alni, Lyne 1983

Figure 25:

Temperatures during 1982 and 1983 at Lyne

——————— 1982

– – – – – 1983

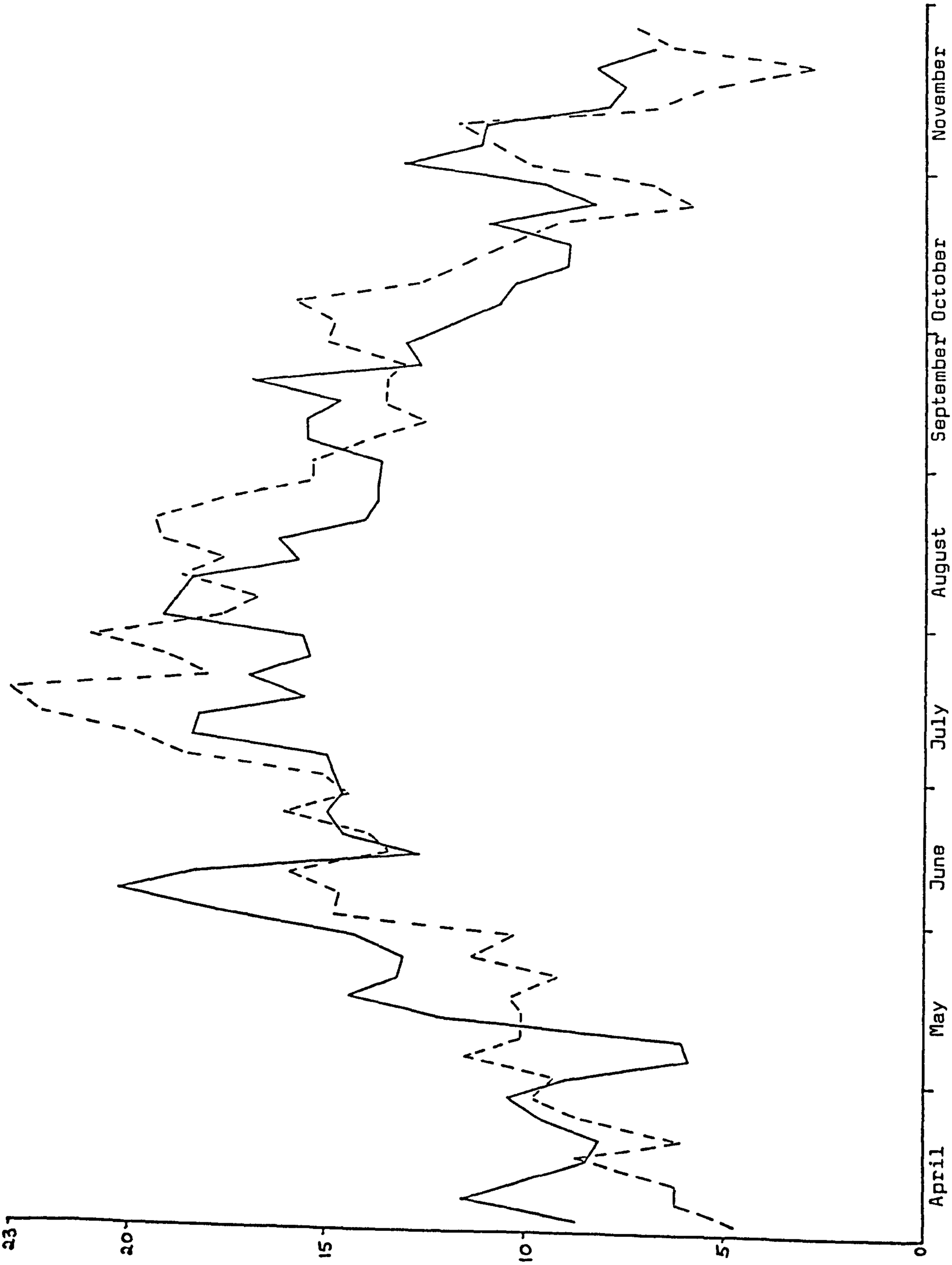

April
May
June
July
August
September
October
November
0
5
10
15
20
23
Twice weekly mean temperature / °C

Figure 26:

Summary of population changes at Lyne,

1982 and 1983

(a) Branch 1

(b) Branch 2

(c) Branch 3

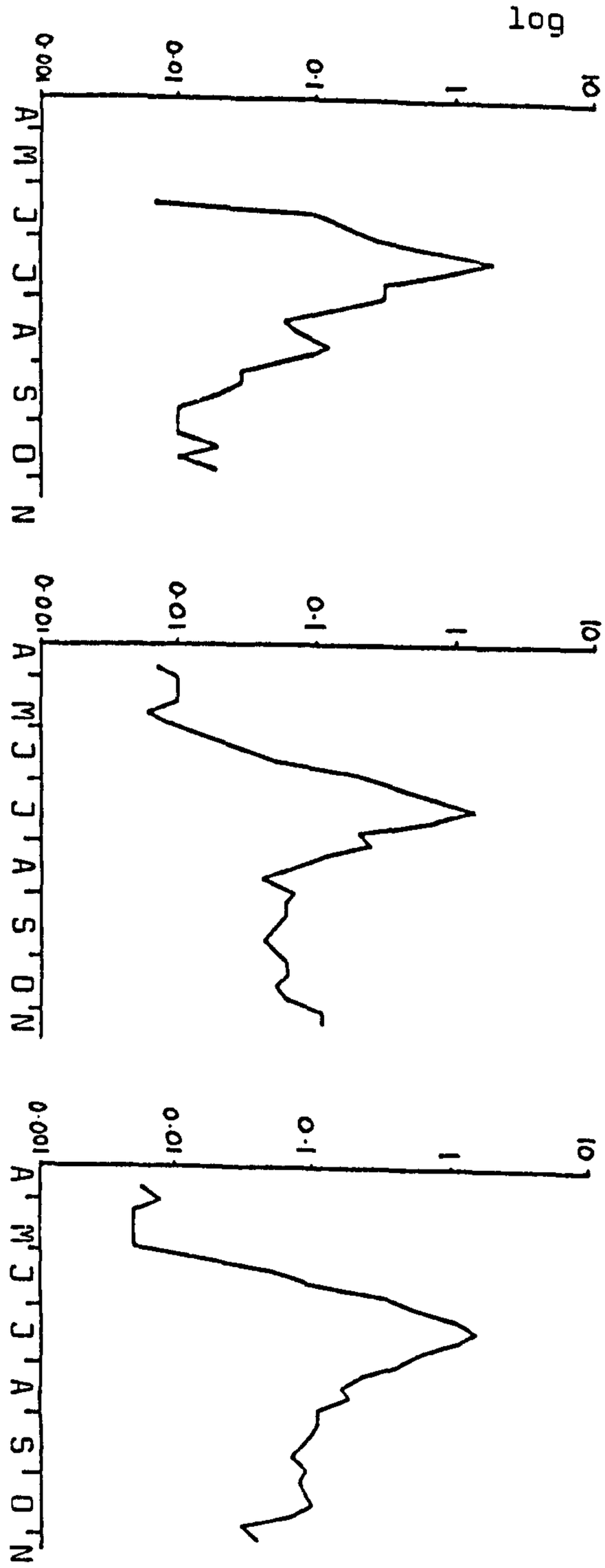
(d) Branch 4

(e) Bush

Top line of graphs : 1982

Lower line: 1983

log aphids per leaf



(a) (b) (c) (d) (e)

/ 4

Table 6 RELATIVE POPULATION GROWTH RATES PER DAY $(LnN_1-LnN_2)(t_2-t_1)^{-1}$
DURING PERIOD OF POPULATION GROWTH - LYNE 1982 and 1983

Date	Branch 1	Branch 2	Branch 3	Branch 4	Bush
1982					
15/4-21/4	0.190	0.290	0.110		0.070
21/4-28/4	0.080	0.030	0.060	0.100	0.070
28/4- 5/5	0.020	0.040	0.050	0.160	0.006
5/5-12/5	0.260	0.200	0.150	0.050	0.140
12/5-19/5	0.180	0.050	0.150	0.090	0.230
19/5-26/5		0.070	0.040	-0.050	-0.004
26/5- 2/6		-0.010	0.020	0.060	0.006
2/6- 9/6		0.030	0.003	0.190	0.030
9/6-16/6		0.040	0.001		0.040
16/6-23/6					
23/6-30/6					
Over total period	0.15	0.08	0.07	0.09	0.07
1983					
20/4-27/4		0.09	0.06		0.09
27/4- 4/5		-0.03	-0.06		0.00
4/5-11/5		0.00	0.00		0.00
11/5-18/5		-0.07	0.00		-0.04
18/5-25/5		0.09	0.00		0.19
25/5- 8/6		0.15	0.38	0.31	0.12
8/6-15/6	0.39	0.11	0.10	0.11	0.16
15/6-22/6	0.07	0.20	0.18	0.24	0.22
22/6-29/6	0.07	0.09	0.07	0.06	0.12
29/6- 5/7	0.14	0.09	0.10	0.03	0.09
5/7-13/7	0.13	0.10	0.05	0.01	0.08
13/7-20/7				0.02	
Over total period	0.16	0.12	0.15	0.11	0.14

by the fundatrices in April/May 1982. A moderate frost (-4.0^{o}C) occurred on April 20th 1983. This coincided with aphid hatch and may have killed any newly hatched aphids on branches 1 and 4. It may also have reduced numbers on the other branches. At a time when the relative growth rates reached their highest values in 1982 of 0.2 and above (population doubling time 3.5 days), the 1983 populations were decreasing or at best, remaining constant. The 1982 populations peaked in early June and at the corresponding time in 1983 the populations were increasing at their most rapid rate; growth rates of 0.38 being recorded (doubling time 1.8 days). Reference to fig.25 shows that during April/May 1982 the temperature was higher than at the same time in 1983. During June 1983 the average temperature was 15^{o}C compared to 7^{o}C in April 1982; the two periods when population growth was occurring. The overall relative growth rates for the populations were generally greater in 1983 than 1982. The value of 0.15 for branch 1 in 1982 is likely to represent a false situation as the population peaked very early due to submergence under flood water. The higher values obtained in 1983 meant that higher peak numbers resulted from lower initial numbers than in 1982.

There was a significant negative correlation between the peak number of fundatrices on a branch and the subsequent peak value of the total population (fig.27, $y = 0.159 - 0.349x$, $r = -0.772$, $p < 0.01$). The fundatrix peak was also related to the timing of the population peak (fig.28, $y = 2.24 - 4.29x$, $r = -0.868$, $p < 0.01$). These figures show that with a relatively high number of fundatrices present in spring the subsequent population peak is earlier and smaller than one when the fundatrices are present in lower numbers.

If the age structure of the populations at their peaks is compared, certain trends emerge (table 7). If branch 1 is not considered for this analysis due to the dubious nature of its peak in 1982, then all populations contained relatively more apterous adults at the time of

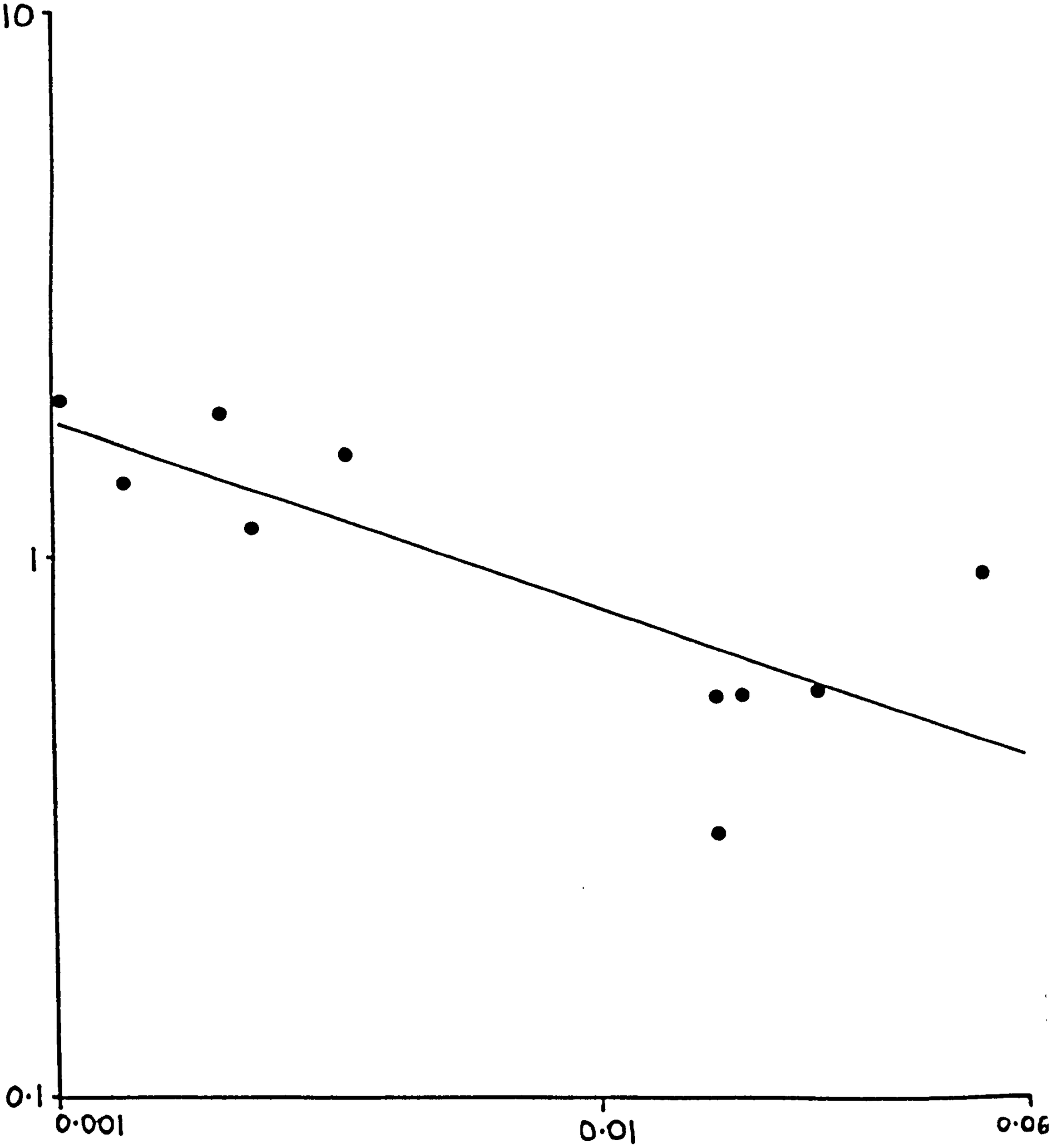


Figure 27: The relationship between the number of fundatrices present in spring and the subsequent total population, Lyne 1982 and 1983

Figure 28:

The relationship between the peak spring number of fundatrices and the time of the subsequent population peak, Lyne 1982 and 1983

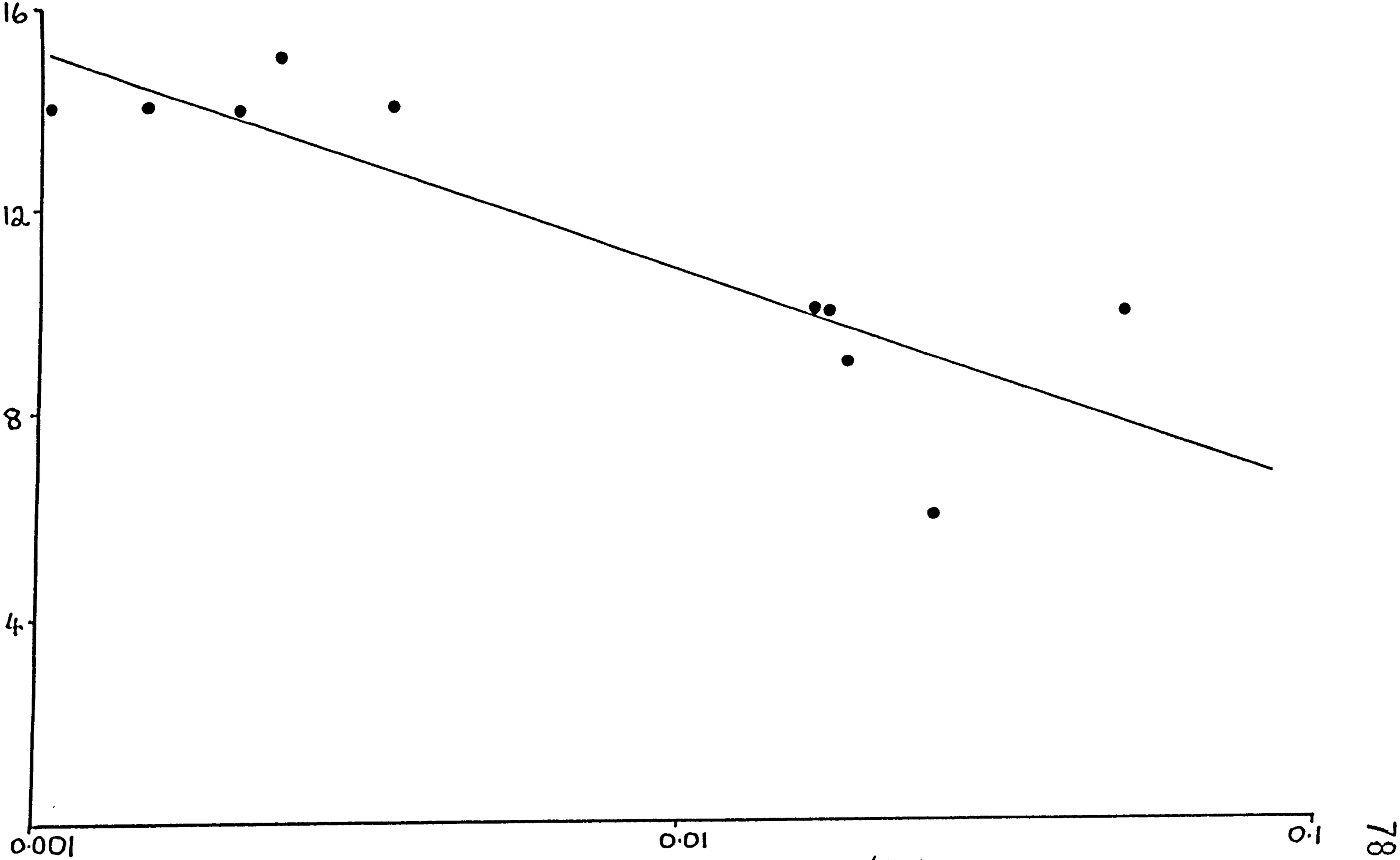

16
12
8
4
Weeks from April 20th
0·001
0·01
0·1
log. peak number of fundatrices per branch / bush

Table 7 AGE STRUCTURE OF POPULATIONS AT THEIR PEAKS - LYNE 1982 and 1983

1982

Branch	Population peak (aphids/leaf)	Nymphs	Proportion of Population IV (apterae)	Apterous adults	IV (alatae)	Alate adults
1	0.56	96.7	0	3.3	0	0
2	0.30	74.3	2.3	7.4	9.7	6.3
3	0.92	73.9	0.9	10.0	12.3	2.9
4	0.55	82.8	0.5	7.7	1.9	7.1
Bush	0.55	66.8	3.3	7.4	18.6	3.9

1983

Branch	Population peak (aphids/leaf)	Nymphs	Proportion of Population IV (apterae)	Apterous adults	IV (alatae)	Alate adults
1	1.95	74.4	0	4.9	13.6	7.1
2	1.39	81.3	0.1	3.5	7.0	8.1
3	1.54	76.9	0	2.6	10.1	10.4
4	1.13	77.4	0	0.4	5.1	17.1
Bush	1.85	76.9	1.5	3.4	13.4	5.0

peaking in 1982 than they did in 1983. Fourth instars (potential apterae) followed a similar though not as consistent trend. Although alatae were produced earlier in 1982 there tended to be less of them in the population at the peak, but this was not consistent with the fourth instars (presumptive alatae). Therefore, lower, earlier populations contain a higher proportion of apterous adults than do higher, later populations.

Thus the timing and extent of the population peak is related to the relative numbers of the fundatrices which hatch in spring. Using autumn leaf samples taken in 1981 a significant correlation exists between the peak number of oviparae present in autumn and the subsequent maximum number of fundatrices which hatch the following spring (fig.29; $y = 1.18x + 1.27$, $r = 0.849$, $p < 0.01$). The relationship between the fundatrices present in spring and subsequent numbers of oviparae is less marked (fig.30; $y = 0.002 - 0.33x$, $r = 0.746$, $p < 0.05$) and may reflect a greater number of mortality factors acting on the aphid populations during summer compared to those acting on the overwintering eggs.

2.4. DISCUSSION

Whilst the pattern of abundance was similar for the bush and all branches sampled, the level and timing of the population peaks varied between the two years.

In both years the decline in the population was due to a fall in the numbers of instars I-III present, although after the drop the proportion of this age group in the population remained fairly stable (figs.4 and 16). The sudden fall in the numbers of these nymphs may be due to

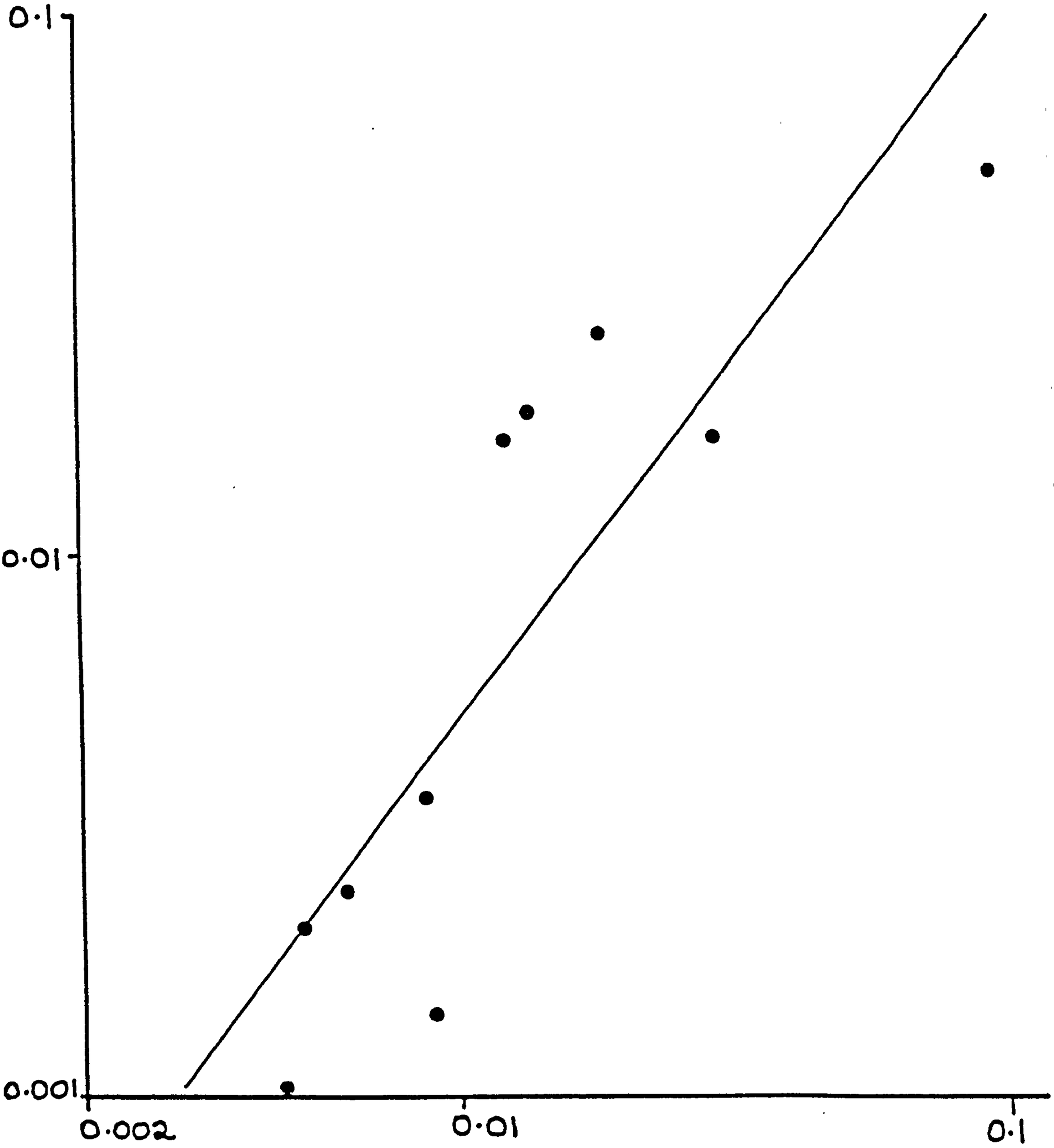


Figure 29: The relationship between autumnal numbers of oviparae and subsequent spring numbers of fundatrices, Lyne 1981 - 1983

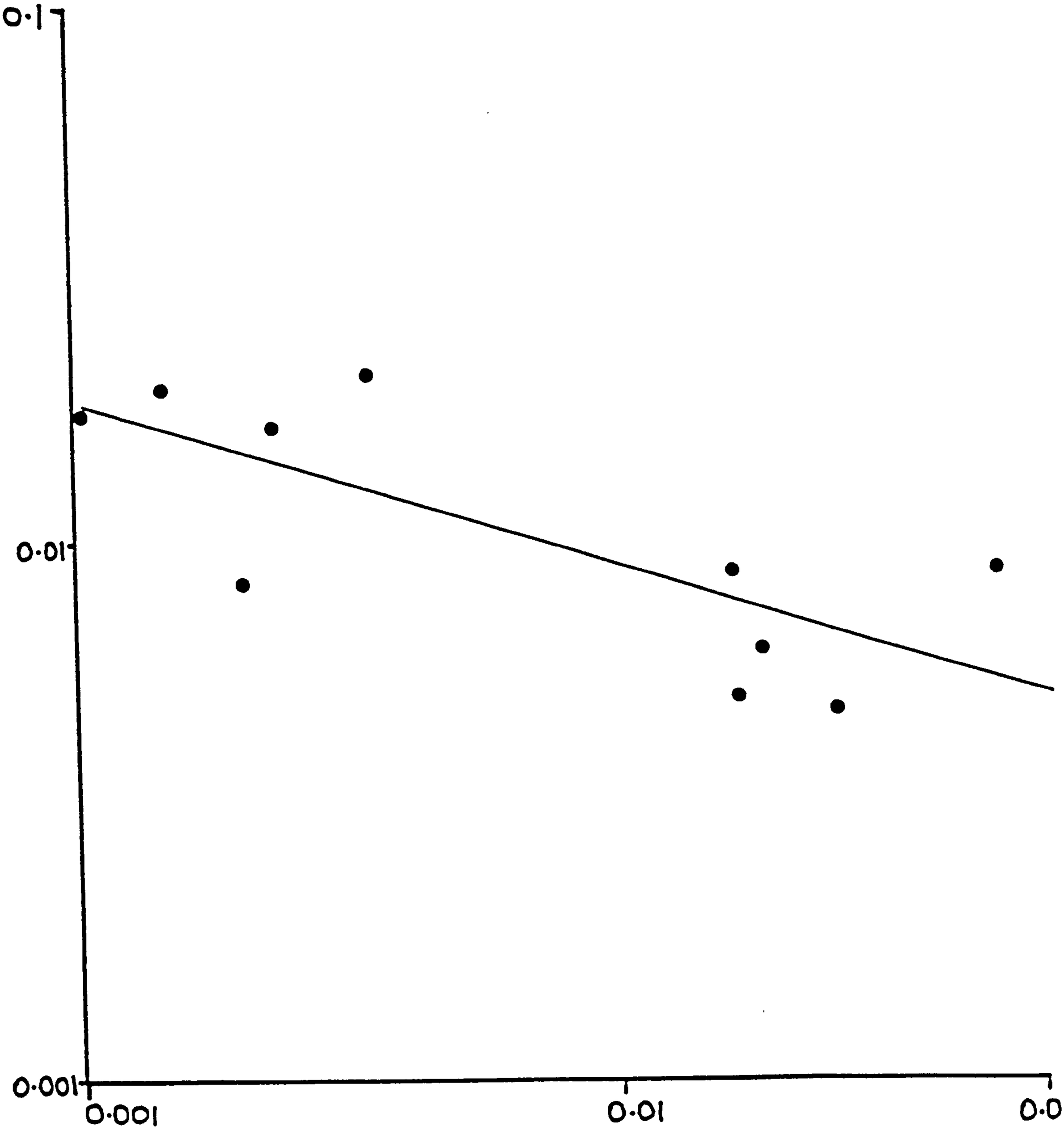


Figure 30: The relationship between spring numbers of fundatrices and subsequent autumnal numbers of oviparae, Lyne 1982 - 1983

1) Nymphal mortality

2) Adult mortality

3) Reduction in reproduction of adults

4) Maturation of nymphs into alatae which emigrate

Natural enemies are unlikely to play a major part affecting the population build up. At the time of the peaks there was an average of 0.7 predators per 100 aphids present in 1982 and 0.8 per 100 in 1983. These figures rose to 20 per 100 in 1982 and 6 per 100 in 1983 after the population decline. Thus it appears that natural enemies may play a role in the maintenance of aphid populations after the decline period.

At the times of the population peaks, numbers of reproducing adults declined. The adults maturing at this time were alate and these appeared to emigrate. Thus the number of nymphs being recruited to the population fell and those present grew up into alate individuals which tended to fly away. Not all the alates flew. A number remained on the leaves and these began reproduction. This tended to stabilize the numbers although the trend was still downwards at this time, a likely cause being the action of predators, now present in higher numbers relative to the aphids than earlier in the season.

The differences in the populations between years appear to have been affected by the early spring temperatures. Temperature can have a considerable effect on the reproduction of fundatrices (Dixon,1971c). The April and May of 1982 were warmer than those of 1983 (fig.25). This combined with the higher numbers of fundatrices present produced higher relative population growth rates at this time than for the comparable period in 1983 (table 6). The population increased earlier and alatae were produced earlier. Due to the fact that these were crowded, flight took place earlier than in 1983. Thus the factors listed above combined to produce population peaks in early June.

In early June 1983 the populations were rapidly increasing (table 6) after a slow start, due to the cold April/May. The second generation was almost entirely apterous, presumably due to the low initial numbers resulting in the fundatrices being less crowded than in 1982. It is reported that apterous aphids are more fecund than their alate counterparts (Dixon and Wratten, 1971). The higher temperatures experienced by these apterous adults and the increased nymphal growth rate combined to produce a rapid population build up and a higher peak than in 1982. Crowded conditions resulted in the next generation being alate. These flew from the alder and together with cessation of reproduction and maturation of nymphs contributed to the rapid decline noticed in mid July. Similar causes of population decline were found for T.annulatus on oak by Lorriman (1980).

The phenomenon of low fundatrix numbers giving a late peak and high numbers an early one was reported for the lime aphid (Dixon, 1971c). However, in that case the late peak was lower than the early one. With P.alni at Lyne the late peak was higher. It is likely that this may be due to the very small populations of P.alni which existed in this locality. The late peak was higher because of reproduction by the apterous adults of the second and third generations. The lime aphid fundatrix numbers reported in Dixon's paper were 20-50 times greater than those recorded at Lyne. Thus when aphid populations are very small, population trends may occur which are different from those at higher densities. It will be reported later that at East Malling where aphid numbers were 30 times those at Lyne the changes in abundance were very similar to those of the lime aphid.

At Lyne, alatae were produced, as a result of crowding, earlier in 1982 and subsequent migration caused the population to decline. Two or more aphids may constitute 'a crowd' (Lees,1966) and thus numbers need not be high for alate production. Analysis of Morisita's index of dispersion

(tables 3 and 5) indicates that the aphids were aggregated throughout the period of population increase. The offspring of alate aphids that colonize plants rarely develop into alatae (Lees 1966). Thus in 1983 the apterous adults produced during June by fundatrices or arriving alates reproduced rapidly to produce peaks in late July. The aphids were more numerous because more apterous adults were produced before alate formation than in 1982. P.alni is facultatively alate which is not the case with E.tiliae, viviparae of which are always winged. P.alni thus appears to exploit a changing habitat in a different way to the lime aphid.

It is interesting to note that the population peaks coincide with the highest recorded mean temperatures during the week in both years (fig.25), these being 20.5°C in 1982 and 23°C in 1983. As rapid increase of the 1983 population occurred during periods of the mean temperature being about 20°C it is unlikely that it is a major factor in the decline. It could contribute however, by increasing activity and thus the tendency of aphids to fly. Temperature was considered a factor contributing to the decline in numbers of C.juglandicola on walnut (Sluss,1967). The temperatures reached 38°C in some orchards in California, however population peaks were reached before the hottest part of the year. Thus it is unlikely that this was the major factor, confirmed by Dixon (1977). The annual peak in numbers of P.alni thus appears to be determined by the number of aphids present at the beginning of the season and the spring temperature. The temperature determines the rate of reproduction and speed of development of the aphids. This is a similar situation to the lime aphid (Dixon,1971c; Barlow and Dixon, 1980).

It has been reported that D.platanoidis induces changes in its host plant leaf quality (Dixon, 1970a) and these may affect its numbers. A large population in spring affects the nitrogen metabolism of the leaves usually resulting in a relatively small population the following autumn.

Dixon (1971b) also reported that infestations of E.tiliae inhibit root growth of lime, cause leaves to contain less chlorophyll and senesce earlier than on uninfested trees. However, it was also reported (Dixon, 1971c) that the changes induced did not appear to be to the aphids' disadvantage. Induced host plant changes affecting aphid numbers were also suggested by Perrin (1974) and Sluss (1967).

The percentage of soluble nitrogen in the leaves is a good indicator of the nutritive quality of this tissue for aphids (Dixon,1971c,d). In general this falls from high spring levels to low values in midsummer, rising again in autumn. In 1982 the population peaked four weeks before the lowest percentage of soluble nitrogen was recorded. In 1983 the peak and lowest percentage coincided. Therefore it does not appear that changes in the host plant contribute significantly to the decline in the aphid numbers. The changes in soluble nitrogen of alder and the possibility of these changes being aphid induced are discussed more fully in chapter 5.

The phenomenon of alder leaves being shed in summer was noted by Kikuzawa (1980), who claimed that for certain alder species, including A.glutinosa, 30-50% of the yearly leaf fall occurred in summer. In the current study this appeared to be about 10% (figs.2 and 14).

Generally at least 50% of the leaves on the branches were uncolonized throughout the season (appendix 1.1,1.2,1.3,1.4,1.5,1.6) so it is unlikely that leaf fall contributed significantly to the population decline.

A measure of changes in numbers between seasons may be obtained from the abundance of fundatrices each spring (Barlow and Dixon,1980). The relationship has been shown to be an inverse one for the lime aphid such that low numbers of fundatrices in year t tend to give rise to higher numbers in year t+1 and vice versa. The result is that populations

tend to oscillate from year to year. The relationship has a summer and a winter component. The summer one is the relationship between fundatrices at the beginning of a season and oviparae at the end and the winter one, oviparae in autumn and fundatrices the following spring. From figs.29 and 30 these two components for the alder aphid are

$$\log O_t = 0.002 - 0.33 \log F_t \quad \text{(summer)}$$

and $$\log F_{t+1} = 1.27 + 1.18 \log O_t \quad \text{(winter)}$$

As described by Dixon (1971c) a population grows on a logarithmic scale from its previous value by the addition of the logarithm of the reproductive rate (R). Thus the expected relationship between autumn oviparae (O) and spring fundatrices (F) would be

$$\log O = \log F + \log R$$

Mortality related to the number of fundatrices can be represented as a negative power F^{-x}, and the relationship becomes

$$\log O = \log F + \log R - x \log F$$

The value of x represents the degree of density dependence. Thus the summer and winter component equations may be presented as

$$\log O_t = \log F_t + 0.002 - 1.33 \log F_t \quad \text{(summer)}$$

$$\log F_{t+1} = \log O_t + 1.27 + 0.18 \log O_t \quad \text{(winter)}$$

where t = year t

and t + 1= year t + 1.

These equations are very similar in form to those described for the lime aphid (Dixon,1971, Barlow and Dixon, 1980). There appears to be an overcompensated density-dependent factor acting within years (summer component). The winter component is density independent with a constant ratio between peak numbers of oviparae and numbers of fundatrices the next spring.

The overcompensated density dependent mortality is likely to be attributed mainly to the production of alatae. The emigration of alatae may be regarded as a mortality factor. Crowding induces alate production in several aphid species, such as B.brassicae, M.persicae and M.viciae (Hille Ris Lambers, 1966; Lees 1966). Large numbers of alatae of A.fabae develop if the aphids are crowded for two generations (Shaw 1970a). More alatae are produced than is necessary to stabilize aphid numbers and this causes the decline in total numbers. It appears that a similar situation occurs with P.alni. As the values of b in Taylor's power law were significantly greater than one (table 2) the aphids were aggregated in their distribution between leaves. The values of the index of dispersion (tables 3 and 5) indicate that this occurred during the period of population build-up. Thus the tendency to aggregate heightens the degree of crowding, even if the total population on a branch is low. Thus the decline may be attributed to the aphid's response to its own numbers and to a lesser extent the action of predators after the population has declined. A study by Brown (1975) of lime aphid populations in an insectary revealed that in the absence of predators and weather, overcompensation within a year still occurs but is less than in the field. The difference is likely to be due to the absence of the mortality factors mentioned. The inverse density dependent factor acting over winter may be due to differences in the quality of oviparae. Following high numbers of aphids the oviparae produced may be smaller and lay fewer eggs than those produced after low early numbers, similar to the lime aphid (Dixon 1971c). Another possible factor is the action of overwintering predators such as coccinellid and anthocorid adults preying on the aphid eggs.

2.4.1. Advantages in dispersal for P.alni

P.alni disperses in summer to colonize other alder trees. Although Theobald (1927) states that this aphid will live on 'oaks above alders, thyme and willowherb under alders' he stated that alatae only fly to other

alder. All attempts to infest such plants failed and aphids died, whether in cages or not. It is likely that the herbaceous plants mentioned by Theobald had aphids on them which had fallen or flown from nearby alder and that these were not feeding and actively reproducing. There are several aphid species living upon oak such as Tuberculoides spp (Stroyan 1977) which at a glance may be confused with alate P.alni. It will be reported later (chapter 5) that alder does not show such a drop in percentage soluble nitrogen as do other trees and no cessation of reproduction occurs due to changes in the host plant. Cessation in nymphal production occurs in midsummer due to the apterae of the early generations reaching the end of their lives. Thus it seems likely that colonizing alatae having flown from crowded alder may find uninhabited trees on which they arrive and begin reproduction, the host plant quality being sufficient to sustain a new population. Such an event was seen to happen with the arrival of alates on branches 1 and 4 in 1983. Aphids were absent until the arriving alates initiated a population. A further advantage in colonizing new trees may be the fact that natural enemies might be fewer on a tree with little or no previous aphid population.

Although only two years data have been obtained from this site, certain trends appear to have emerged. However, a longer term study is needed to establish the true nature of these trends. This is unfortunately not possible using the sampled branches as the site was partially destroyed during the winter of 1983/84.

2.5. RESULTS AT EAST MALLING

2.5.1. LF125 and LF126, 1982.

(i) Abundance of aphids, LF125

On LF125 (A.glutinosa) overwintering eggs hatched in late April to produce fundatrices. These were adult and reproducing by late May and numbers were growing rapidly. On June 1st a nearby line of ornamental trees were sprayed with an aphicide. Drift onto the windbreak occurred and the population suddenly fell, this being recorded on the next sampling date, June 3rd (fig.31a). The population began to increase until the windbreak was pruned between July 15th and 22nd. This appeared to reduce the numbers considerably and there followed a period of low irregular numbers. During September aphids increased quite dramatically to assume values second only to those before spraying (table 8).

The pattern of abundance on terminal and non terminal leaves was similar and mirrored that of the total population (fig.31b). There were greater numbers of aphids on non terminal leaves for most of the season. However if the aphids present are expressed as numbers per unit area, obtained using the weekly leaf area calculations, the picture is a different one. The population density thus obtained was for the greater part of the year higher on terminal leaves than non terminal (fig.32). Thus although there were more aphids per leaf on non terminals, they were more closely spaced on the terminals, due to the smaller leaf area. After leaf growth had ceased in early July the average terminal leaf area was $10.8cm^2$ whilst that of non terminals was $57.7cm^2$, a significant difference ($d=42.74$, $p<0.001$).

Due to the spraying in early season the age structure histogram (fig.33) does not show complete generations through the season. The apterous fundatrix generation is obvious and the second generation appears to have

Figure 31:

Aphid abundance on LF 125, East Malling, 1982

(a) 200 leaf sample

(b) 100 leaf samples

- - - terminal leaves

——— non-terminal leaves

Arrow represents date of pruning

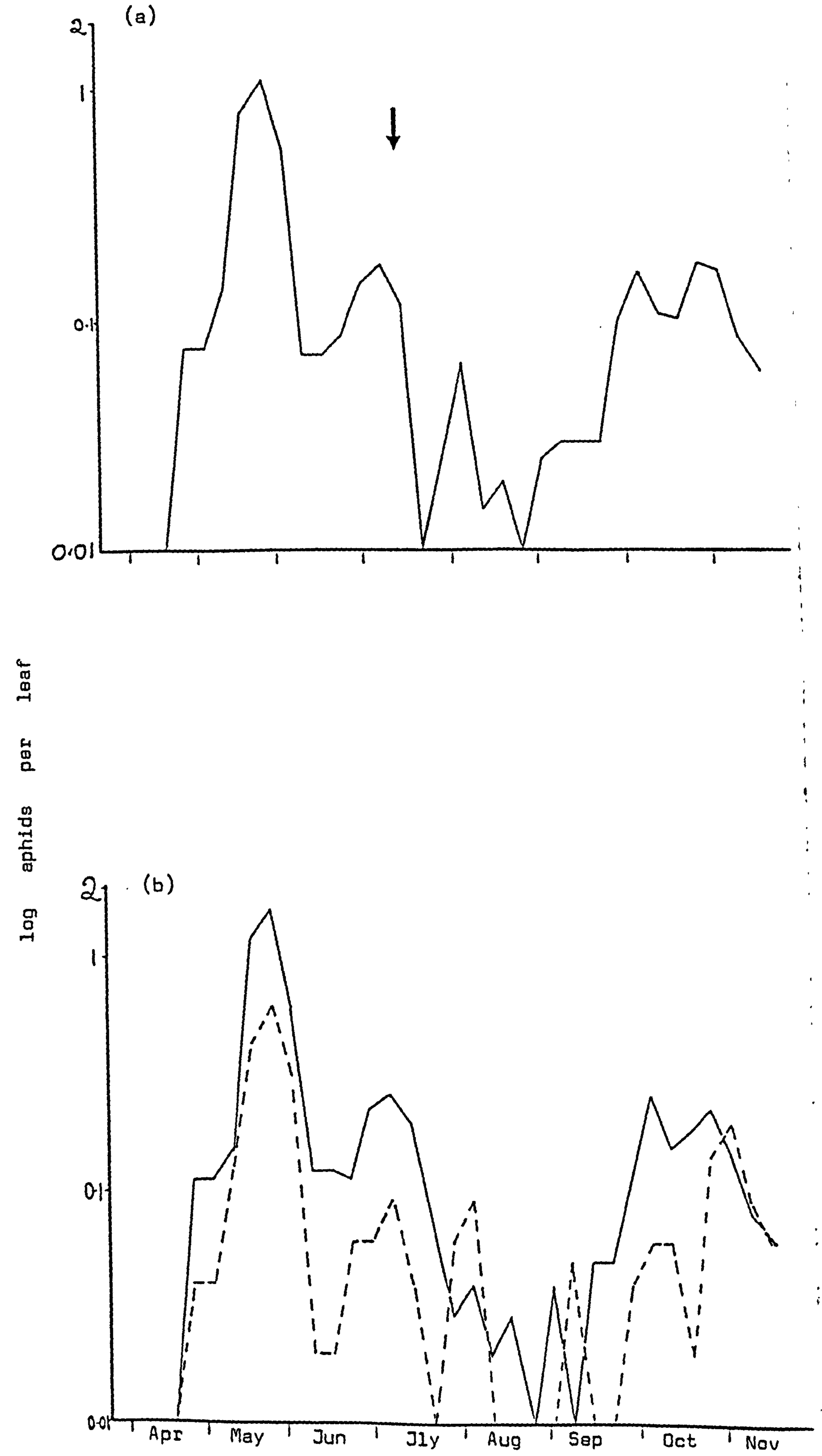

(a)
2
1
0·1
0·01
log aphids per leaf
(b)
2
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Table 8 TOTAL NUMBER OF APHIDS IN LEAF SAMPLES - LF125, 1982

Date	Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample
April 29	3	10	13
May 6	3	10	13
13	11	14	25
20	44	116	160
27	60	157	217
June 3	32	60	92
10	1	11	12
17	1	11	12
24	5	10	15
July 1	5	21	26
8	8	24	32
15	3	18	21
22	0	0	0
29	5	2	7
Aug 5	8	3	11
12	0	1	1
19	0	2	2
26	0	0	0
Sept 2	0	3	3
9	4	0	4
16	0	4	4
23	0	4	4
30	3	15	18
Oct 7	5	25	30
14	5	14	19
21	1	17	18
28	13	20	33
Nov 4	18	13	31
11	8	7	15
18	5	5	10

Figure 32:

The population density of P.alni on LF 125
during 1982

- - - Terminal leaves

——— Non terminal leaves

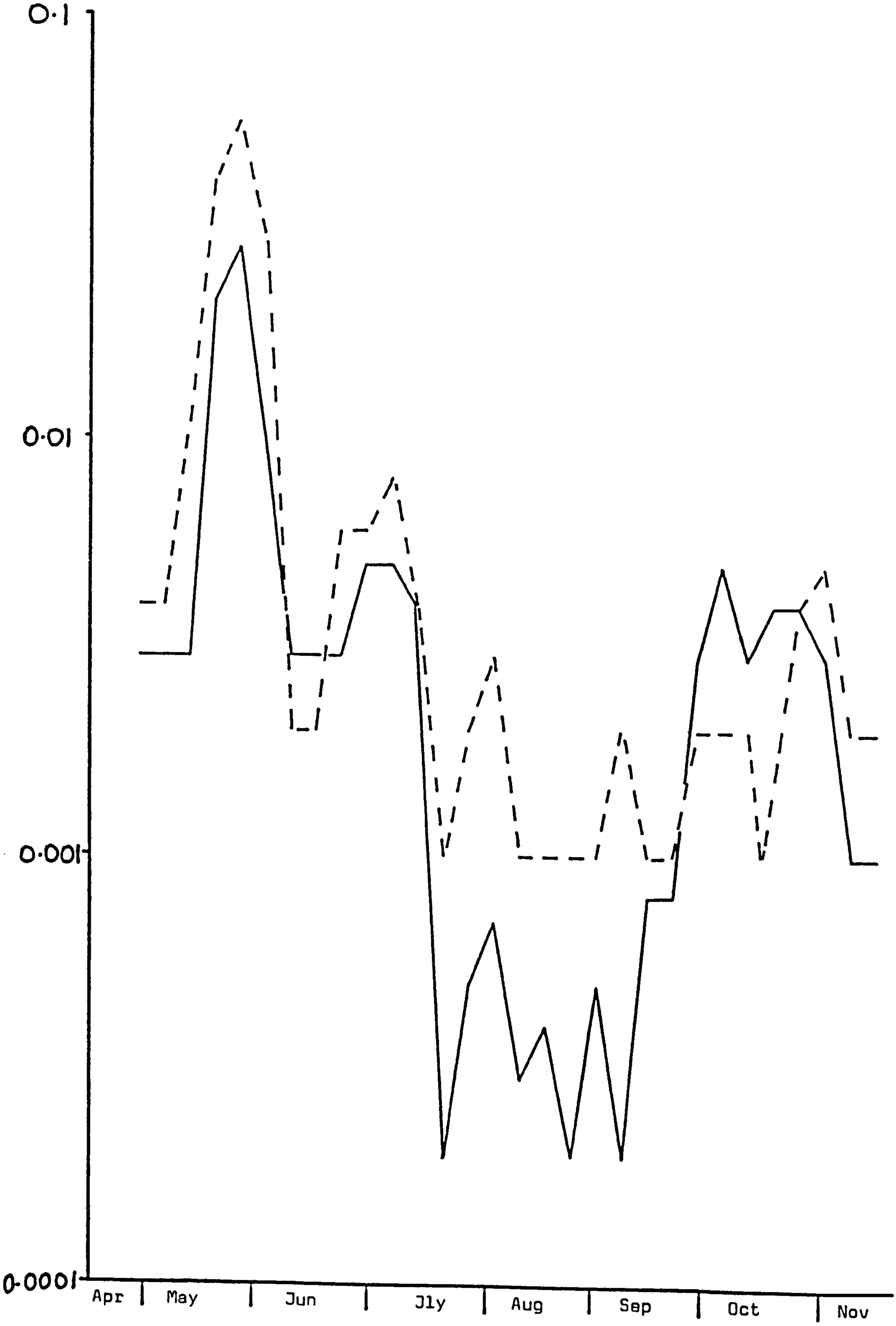

0·1
0·01
0·001
0·0001
log aphids per cm² of leaf
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 33:

Age structure of the population on LF 125, 1982

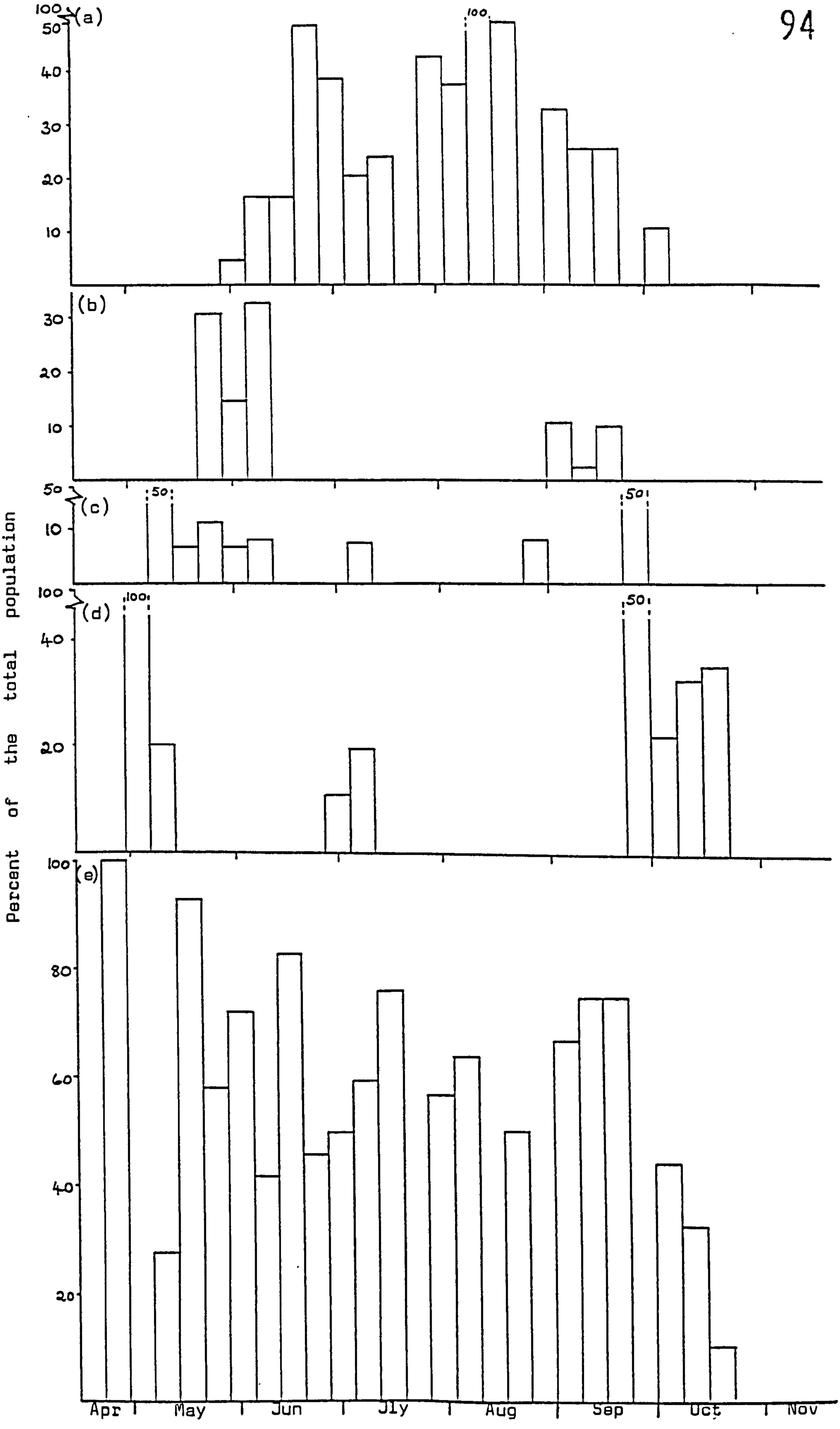
(a) Alate adults

(b) Fourths (presumptive alatae)

(c) Apterous adults

(d) Fourths (presumptive apterae)

(e) Nymphs

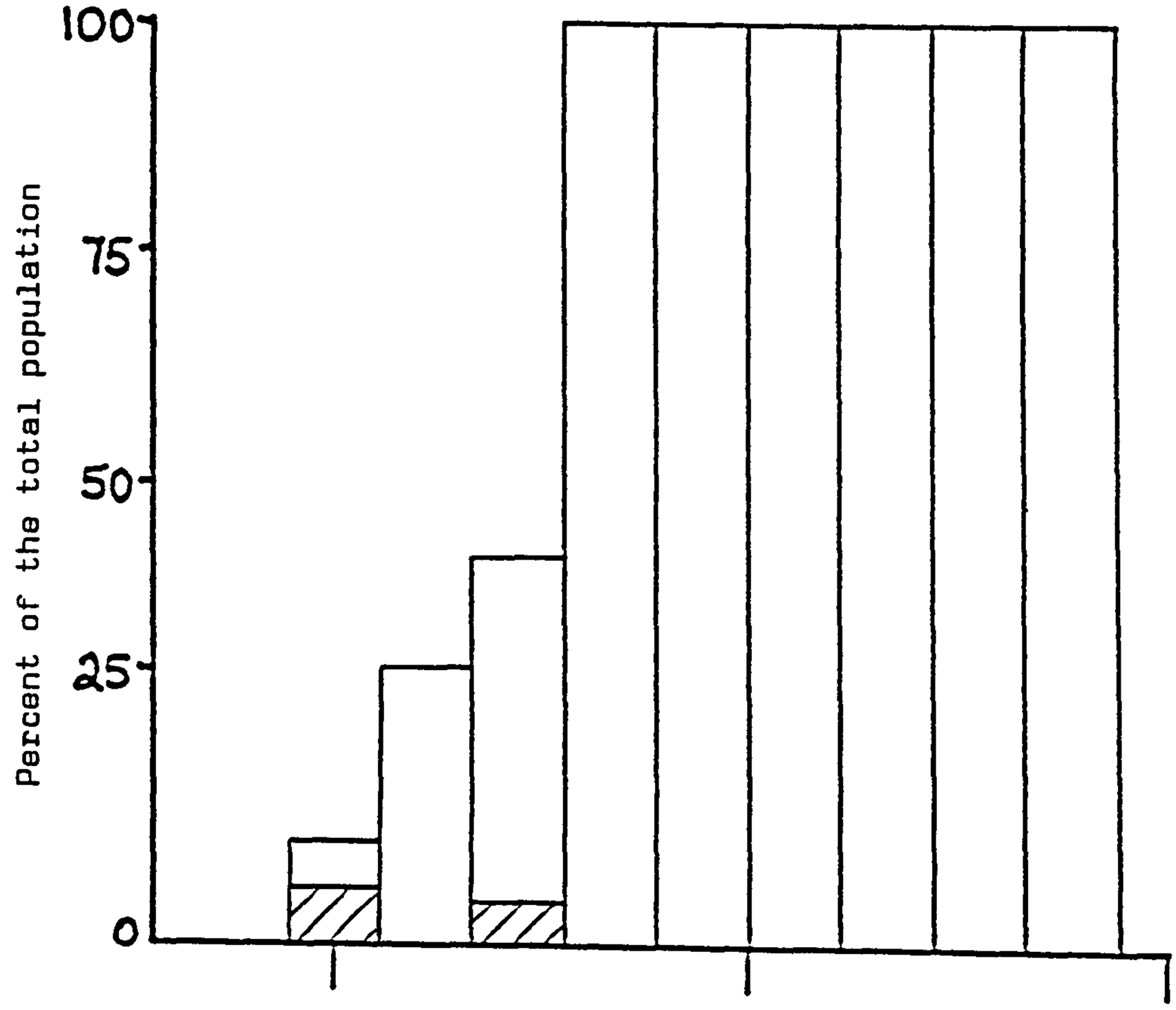

(a)
100
50
40
30
20
10
100
(b)
30
20
10
50
(c)
50
10
50
100
(d)
100
40
20
50
Percent of the total population
100
(e)
80
60
40
20
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

been mostly alate. These were present as fourth instars when the spraying occurred. Some of them matured to produce the early peak in alate numbers. The few alates present appeared not to fly but stayed and began reproducing. The nymphs produced grew up to become apterous adults. Numbers began to increase again but were then reduced after pruning the 15th and 22nd of July. Subsequently the population consisted only of alate adults which began reproducing. The nymphs grew up to be apterous and the offspring of these were the sexual generation. The age structure of the populations on the terminal and non terminal leaves were much the same (appendix 2.1) but the analysis is suspect due to the low numbers of aphids which existed.

Fourth instars (presumptive alatae) first appeared in late May. Their abundance was apparently terminated by spraying and none were found from mid June until the presumptive males appeared in late September. Adult males were only found in early October together with oviparae which persisted until leaf fall in late November (fig.34a). Relatively large numbers of oviparae were present and these reached a peak in late October (fig.34b).

(ii) Spatial distribution of aphids

The value of b in Taylor's power law was 1.47 for terminal leaves and 1.49 for non terminals over the season (table 26). Both these values are significantly greater than one, indicating that the aphids were aggregated. The inconsistencies in the value of Morisita's index through the season is caused by the often low numbers of aphids present (table 9). However it reflects the fluctuations in numbers of aphids. When adults present began reproducing and the population increased the index increased as the aphids were aggregated in small groups. When few aphids were present the index became zero as the aphids present were distributed one to a leaf.


100
75
50
25
0
Percent of the total population

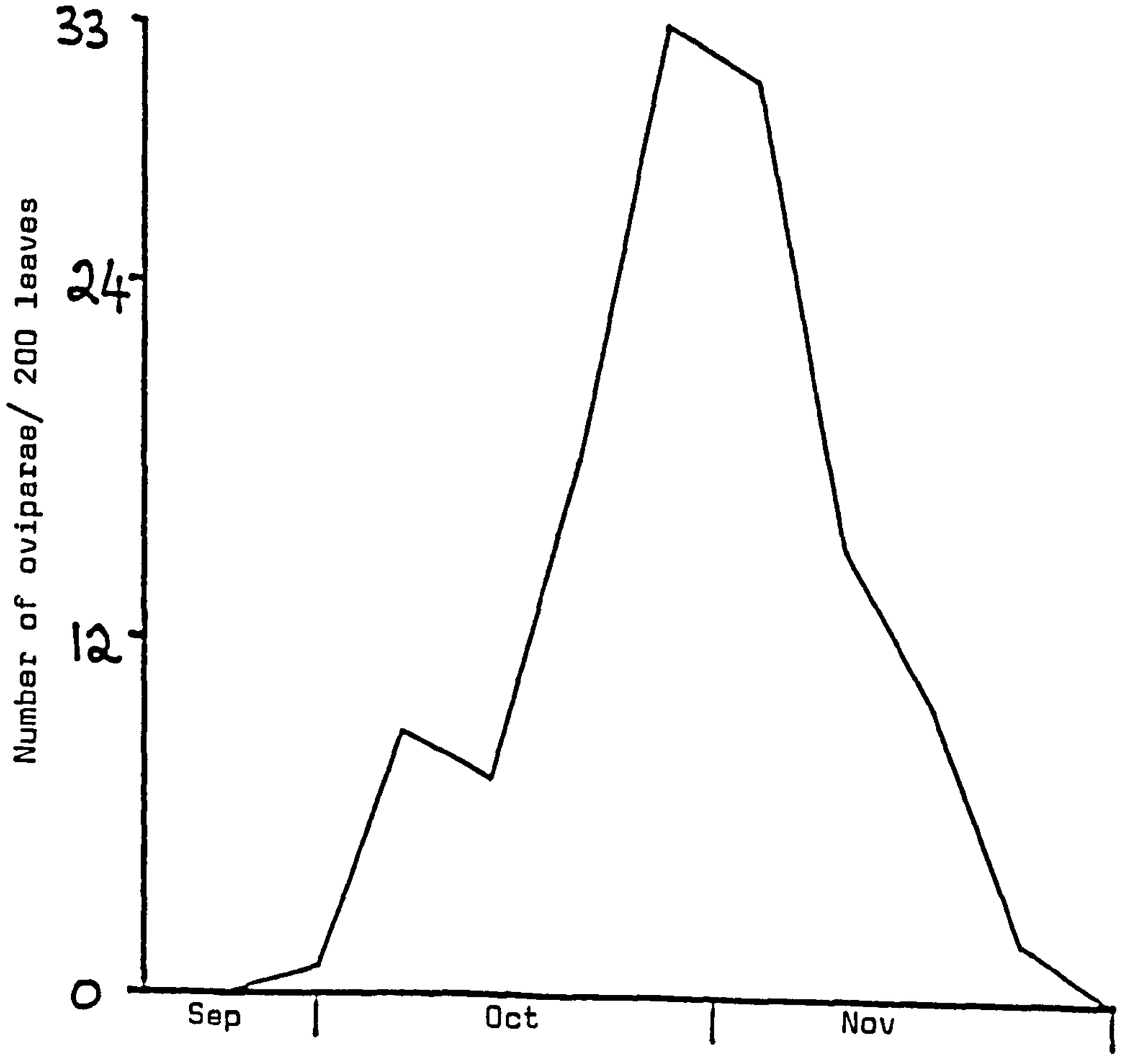

33
24
12
0
Number of oviparae/ 200 leaves
Sep
Oct
Nov

Table 9 MORISITA'S INDEX OF DISPERSION - LF125, 1982

Date		Terminal leaves	Non-terminal leaves
April	29	0	15.6
May	6	0	6.7
	13	10.9	8.8
	20	15.3	13.7
	27	9.3	5.4
June	3	6.7	9.7
	10	0	7.3
	17	0	0
	24	60.0	13.3
July	1	0	7.1
	8	28.6	1.8
	15	0	7.2
	22		
	29	10.0	0
Aug	5	39.3	33.3
	12		0
	19		0
	26		
Sept	2		0
	9	50.0	
	16		
	23		0
	30	33.3	6.7
Oct	7	10.0	7.3
	14	0	4.4
	21	0	2.1
	28		6.4
Nov	4		5.3
	11	53.6	4.8
	18	0	0

(iii) Abundance of natural enemies

The total numbers of predators are shown in fig.35. The ratio of predators to aphids fell as the aphid population increased. However when the aphid numbers were reduced to very low levels, first by spraying and then by clipping, the predator/aphid ratio rose, reaching 1:1 in mid August (fig.36). Adults of A.bipunctata and A.nemorum appeared in mid May. A.bipunctata was the only coccinellid recorded during the year. A.nemoralis was recorded very occasionally through the summer. The commonest predator was B.anqulatus, comprising 53% of total numbers recorded. The second commonest predator was Orthotylus marginalis Reuter, the dark green apple capsid, accounting for 17% of the total. Anthocorids comprised 11% of the predators found (fig.37).

O.marginalis appeared as nymphs in early May. Numbers were steady until spraying occurred and no specimens were found subsequently. In contrast, B.angulatus first appeared in early July. Numbers increased and although declining slightly after pruning this was not as dramatic as the decline in aphid numbers. Adults appeared from late July onwards and females persisted until late September (fig.38). P.ambiguus was recorded in small numbers during June and Pilophorus perplexus Douglas and Scott occasionally during August. C.carnea was recorded on only three occasions during the season, as an adult in October and as larvae during July. Larvae of the cecidomyiid A.aphidimyza were only found on two occasions.

Parasitism, determined by the number of adults containing a parasite larva in random weekly samples of fifty aphids, first occurred in early June (fig.39). This reached a peak of 12% on June 10th and declined thereafter with a small resurgence in mid July. Identification of the wasps which emerged from mummies indicated that the aphids were mainly parasitized by T.pallidus but a few characteristic 'raised mummies' (Blackman,1974) made by a species of Praon were found in the leaf samples. No incidences

Figure 35:

Total number of predators on LF 125
during 1982

Figure 36:

Ratio of predators to aphids on LF 125
during 1982

Figure 37:
Relative abundance of predators by classes on
LF 125 during 1982

(1) Coccinellidae
(2) Anthocoridae
(3) B.angulatus
(4) P.ambiguus
(5) O.marginalis
(6) P.perplexus
(7) Chrysopidae
(8) Cecidomyiidae

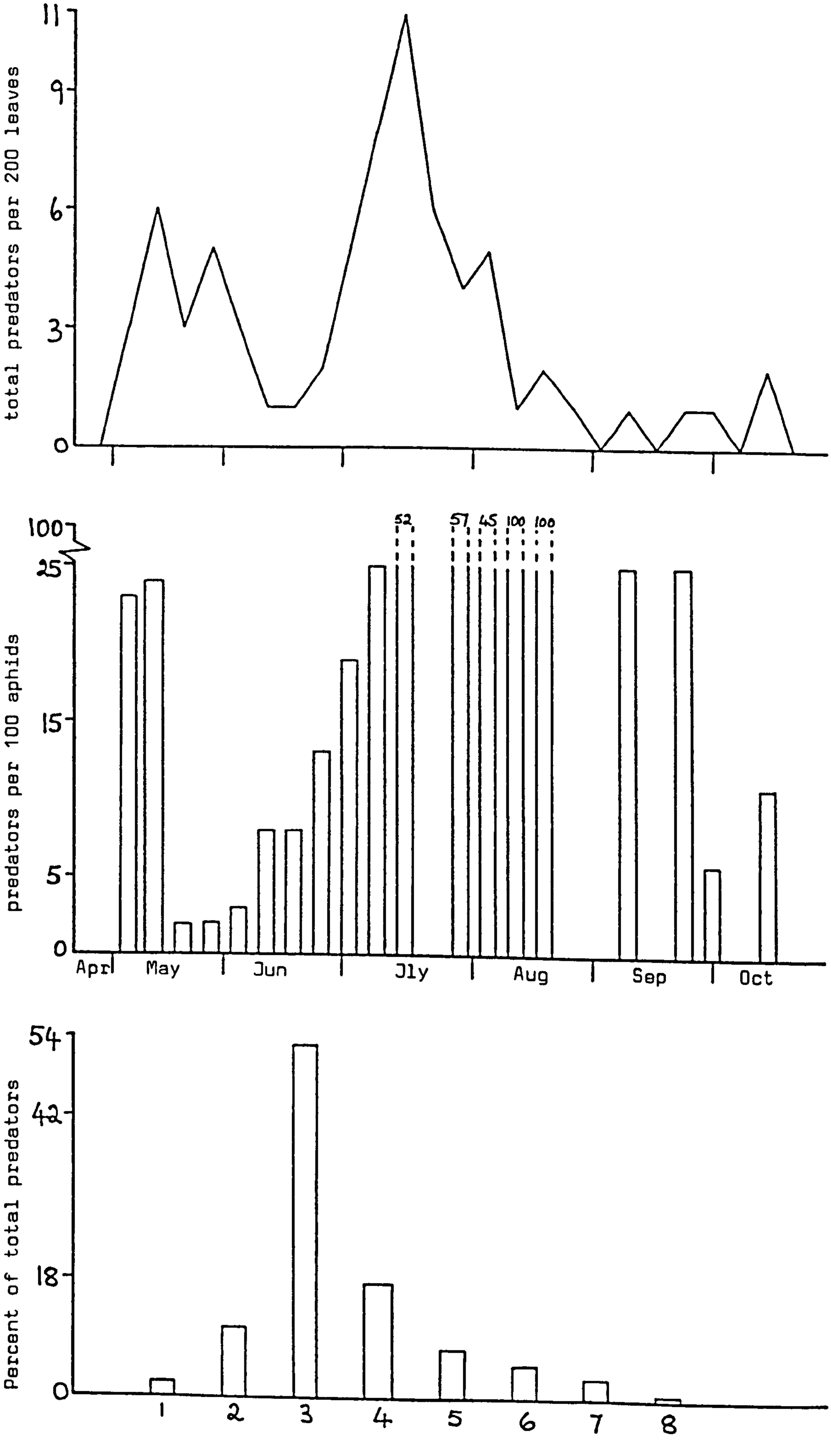

total predators per 200 leaves
11
9
6
3
0
predators per 100 aphids
100
25
15
5
0
52
57
45
100
100
Apr
May
Jun
Jly
Aug
Sep
Oct
Percent of total predators
54
42
18
0
1
2
3
4
5
6
7
8

Figure 38:

Abundance of B.angulatus on LF 125 during 1982

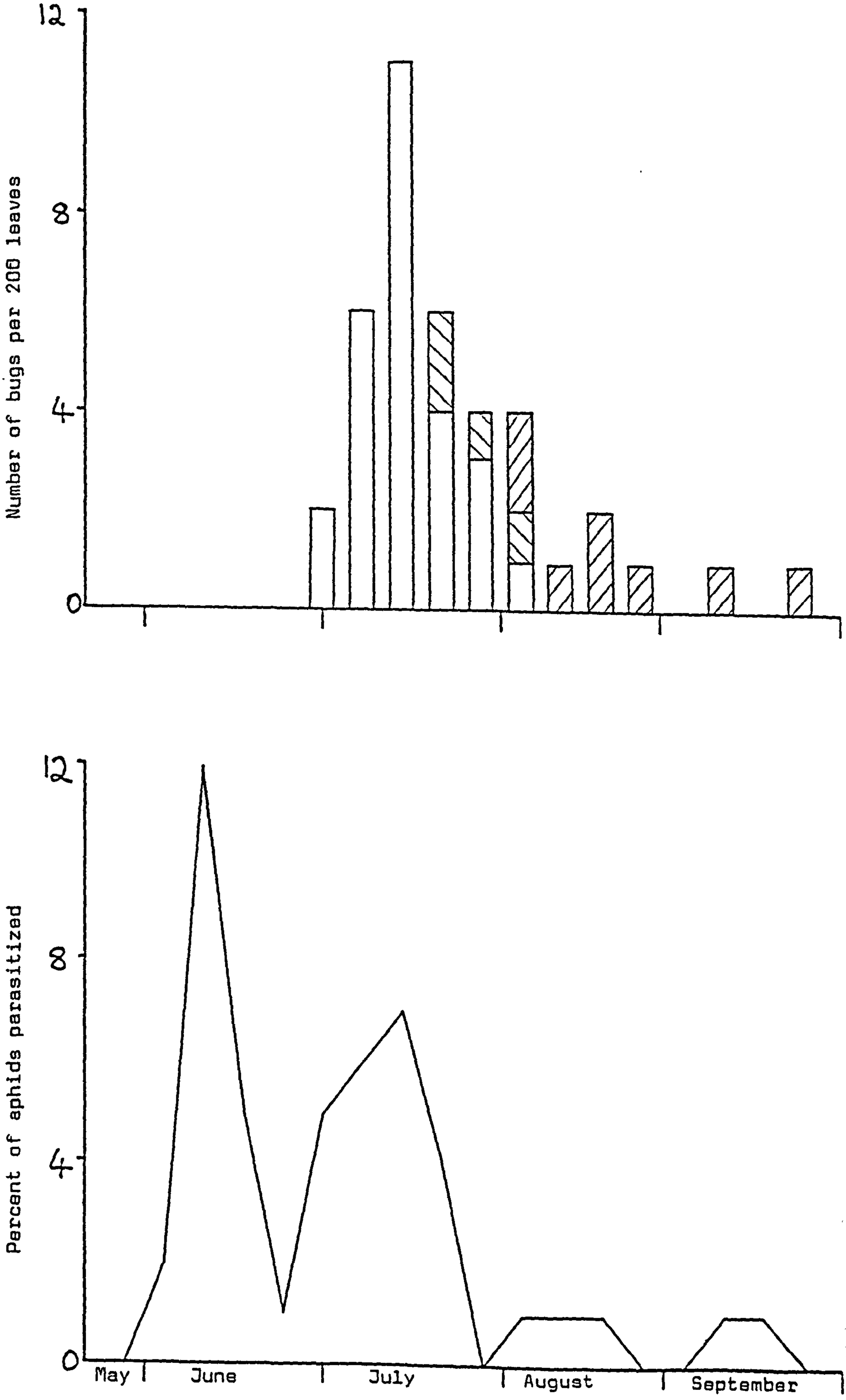
☐ Nymphs

▨ Males

▨ Females

Figure 39:

Parasitism in populations of P.alni on LF 125, 1983


Number of bugs per 200 leaves
12
8
4
0
Percent of aphids parasitized
12
8
4
0
May
June
July
August
September

of aphids being killed by entomopathogenic fungi were recorded.

(iv) LF126, 1982

No aphids were found on the A.cordata and A.incana trees in this windbreak throughout April and May. During June occasional alates were found. On arrival, these began reproducing, causing small population peaks. All aphids had disappeared by mid July (fig.40 a,b). The only predators found were single adult males of B.angulatus, recorded on three occasions during August.

2.5.2. LF125 and LF126, 1983

(i) Abundance of aphids, LF125

The ornamental trees were removed during the winter and the windbreak received no apparent spray drift in 1983. The windbreak was divided into two sections at the beginning of the season. One section was pruned as normal between July 25th and August 1st and the other section was left unpruned.

Aphids were first recorded in late April. Adult fundatrices appeared by mid-May and the populations began increasing rapidly with the onset of reproduction by these adults. (figs.41a and 42a). The populations reached their peaks in early July and the subsequent decline was extremely rapid. The numbers recovered on both sections during October and final numbers were similar on each section (table 10).

The pattern of abundance on both terminal and non terminal leaves was similar to that of the total population (figs.41b and 42b). Aphid density was considerably higher on terminal leaves throughout the period of leaf growth and population build up, (fig.43 a and b). Later in the season when aphid numbers were much lower and the terminal leaves were no longer young this trend was reversed.

Figure 40 (a) :

Aphid numbers on LF 126, A.incana, 1982

Figure 40 (b) :

Aphid numbers on LF 126, A.cordata, 1982

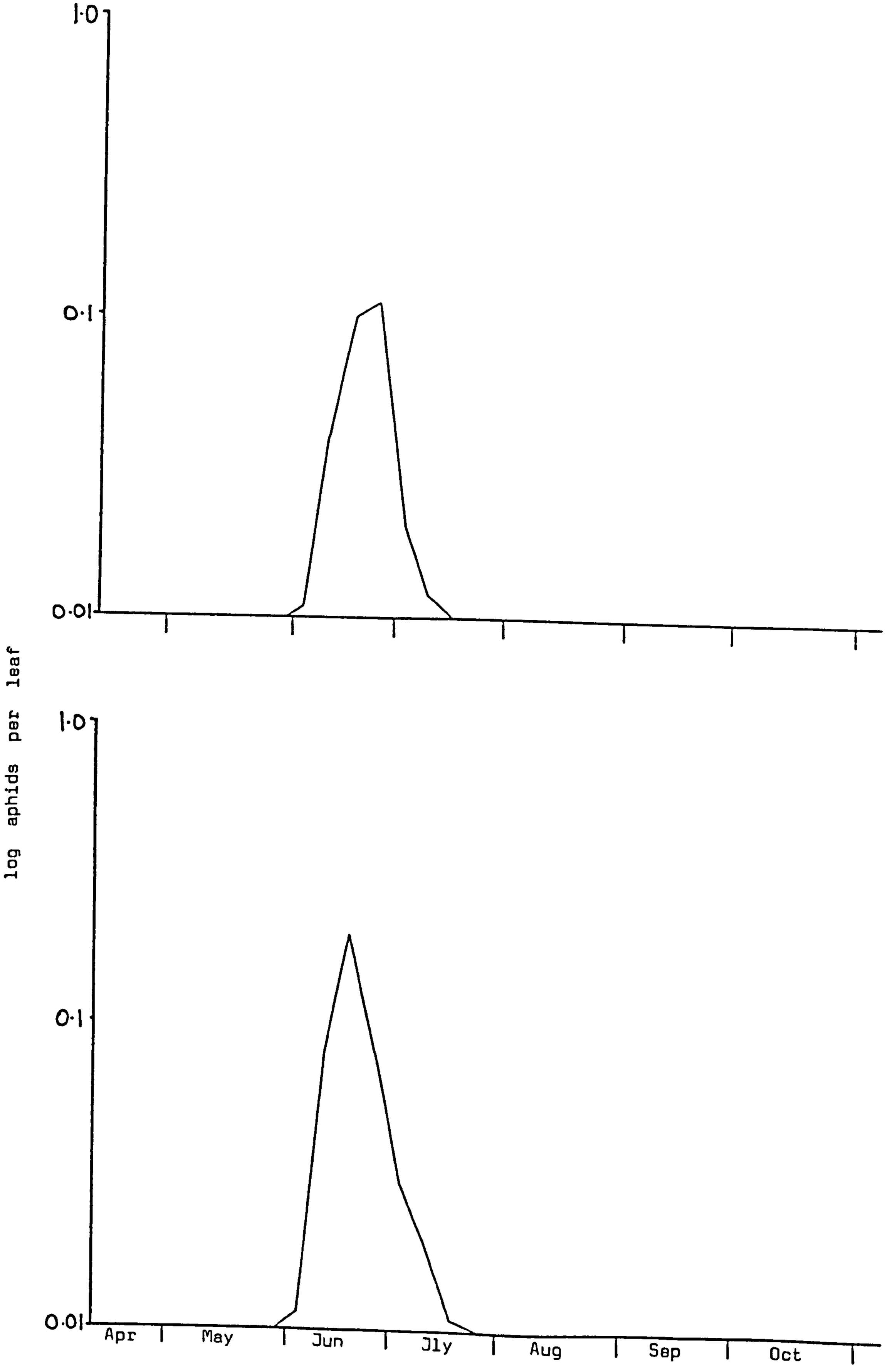

log aphids per leaf
1·0
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 41:

Aphid abundance on LF 125, section 1, 1983

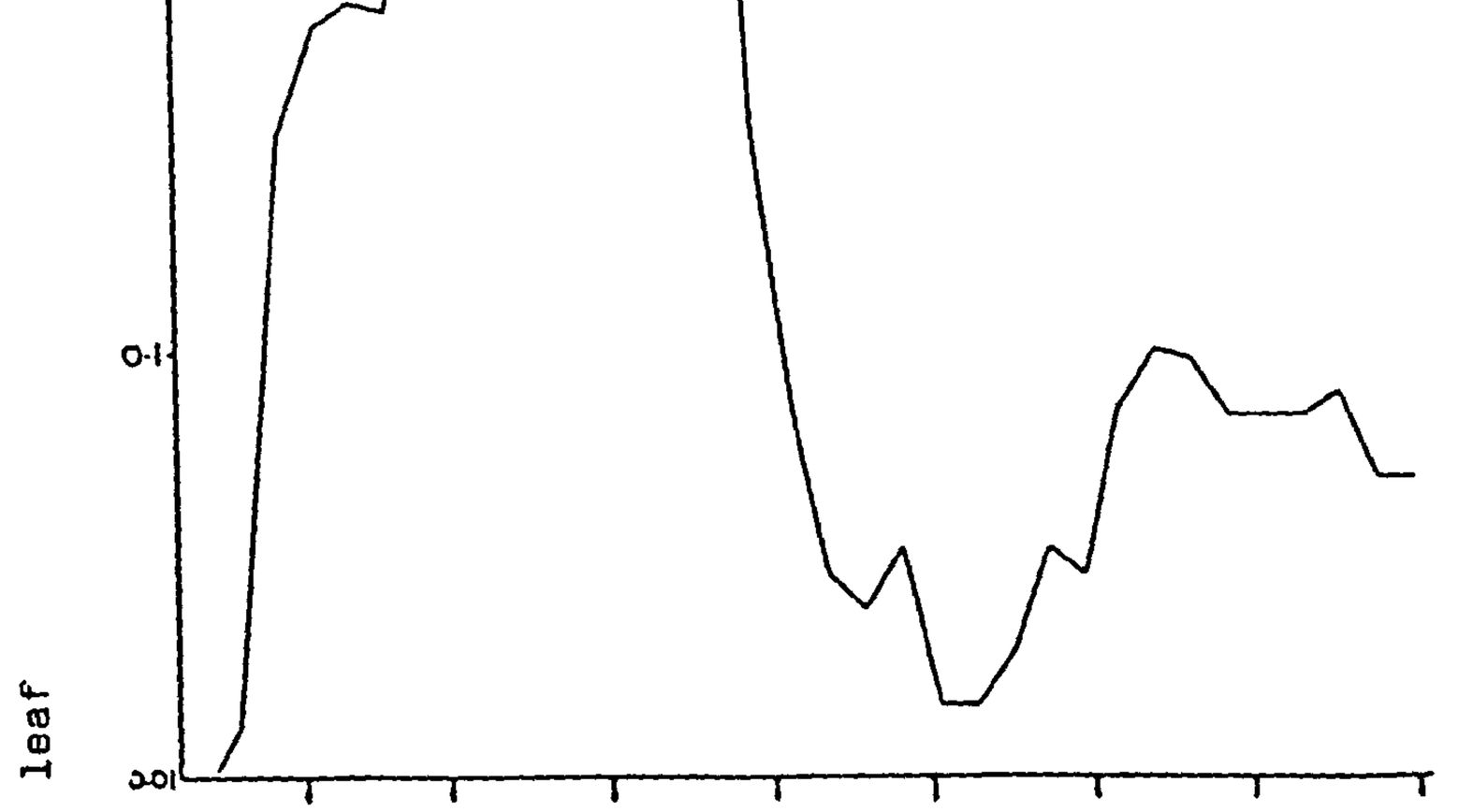
(a) 200 leaf sample

(b) 100 leaf samples:

- - - Terminal leaves

——— Non-terminal leaves

(a)


10
1
0·1
0·01
log. aphids / leaf

(b)

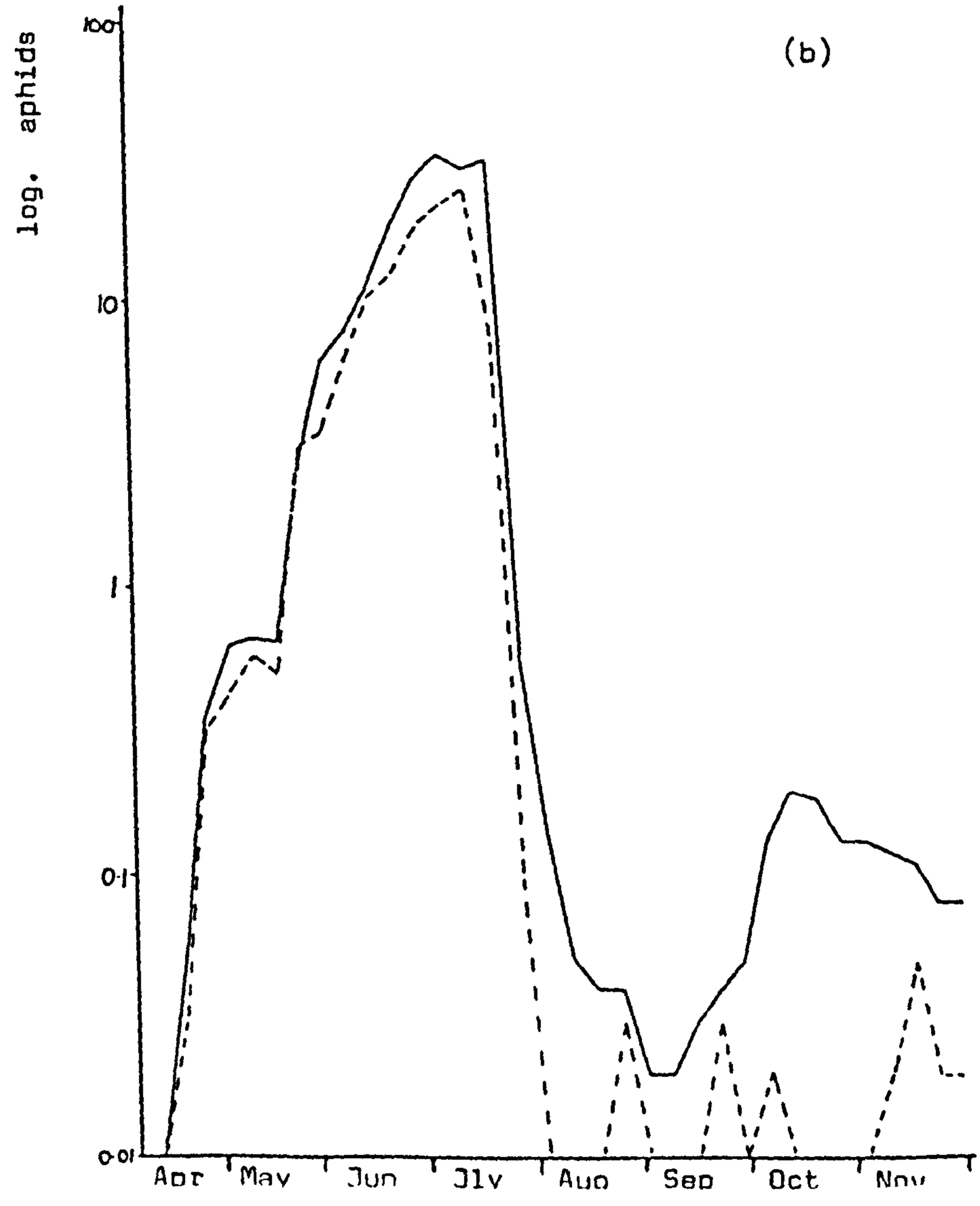

10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 42:

Aphid abundance on LF 125, section 2, 1983

(a) 200 leaf samples

(b) 100 leaf samples:

--- Terminal leaves

—— Non-terminal leaves

Arrows represent date of pruning

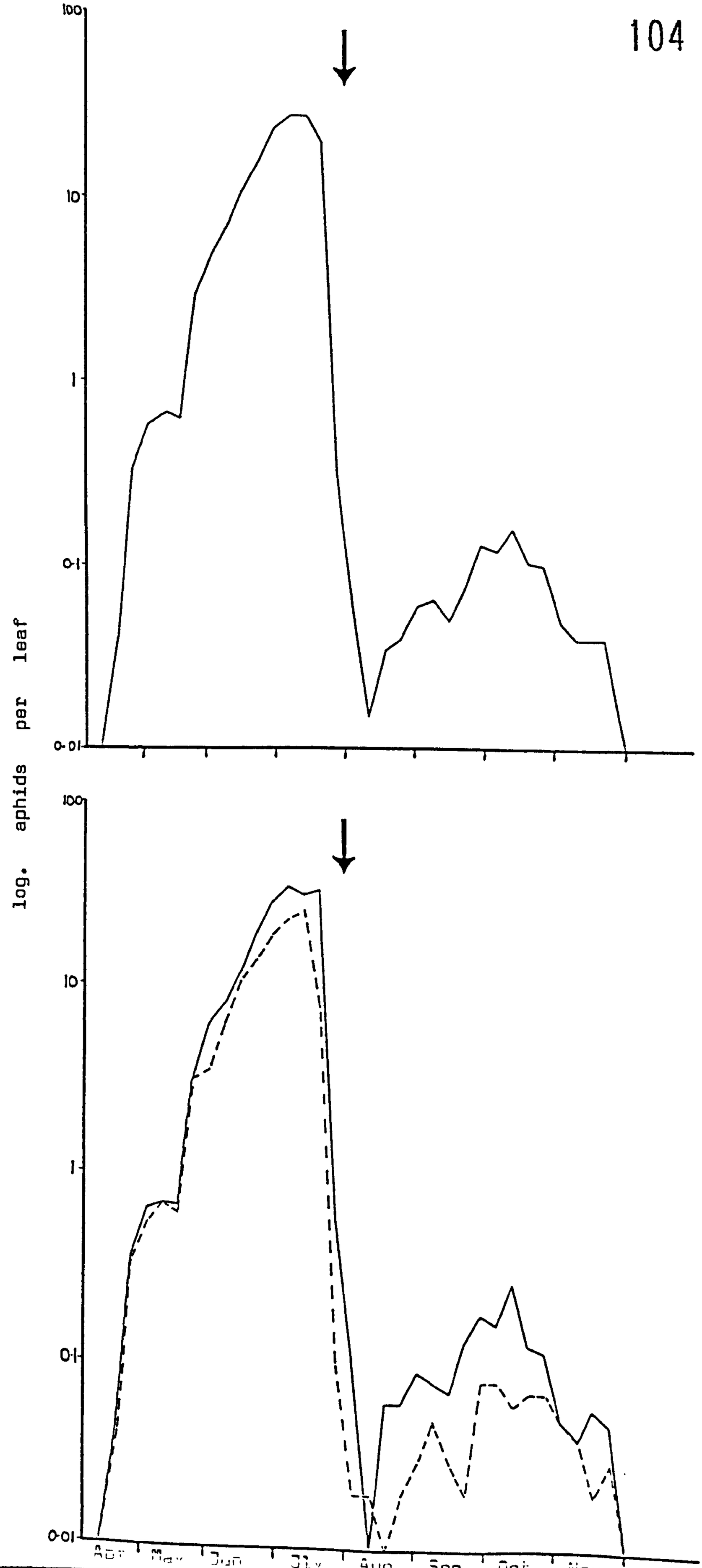

log. aphids per leaf
100
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Table 10 TOTAL NUMBER OF APHIDS IN LEAF SAMPLES - LF125, 1983

Date		S E C T I O N 1			S E C T I O N 2		
		Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample	Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample
April	25	32	34	66	24	36	60
May	2	53	63	116	61	53	114
	9	67	6	133	64	78	142
	16	59	65	124	60	80	140
	23	312	271	583	301	269	570
	30	349	602	951	361	572	933
June	6	615	770	1385	601	798	1399
	13	1029	1120	2149	1110	909	2019
	20	1252	1863	3115	1189	1826	3015
	27	1851	2783	4634	1742	2947	4689
July	4	2206	3360	5566	2119	3523	5642
	11	2508	3000	5508	2475	2854	5329
	18	753	3208	3961	699	3183	3882
	25	9	57	66	4	78	82
Aug	1	0	13	13	1	9	10
	8	0	4	4	1	0	1
	15	0	3	3	0	5	5
	22	2	3	5	1	5	6
	29	0	1	1	2	8	10
Sept	5	0	1	1	4	7	11
	12	0	2	2	2	6	8
	19	2	3	5	1	12	13
	26	0	4	4	7	17	24
Oct	3	1	12	13	7	15	22
	10	0	18	18	5	27	32
	17	0	17	17	6	13	19
	24	0	12	12	6	12	18
	31	0	12	12	4	4	8
Nov	7	1	11	12	3	3	6
	14	4	10	14	1	5	6
	21	1	7	8	2	4	6
	25	1	7	8	0	0	0

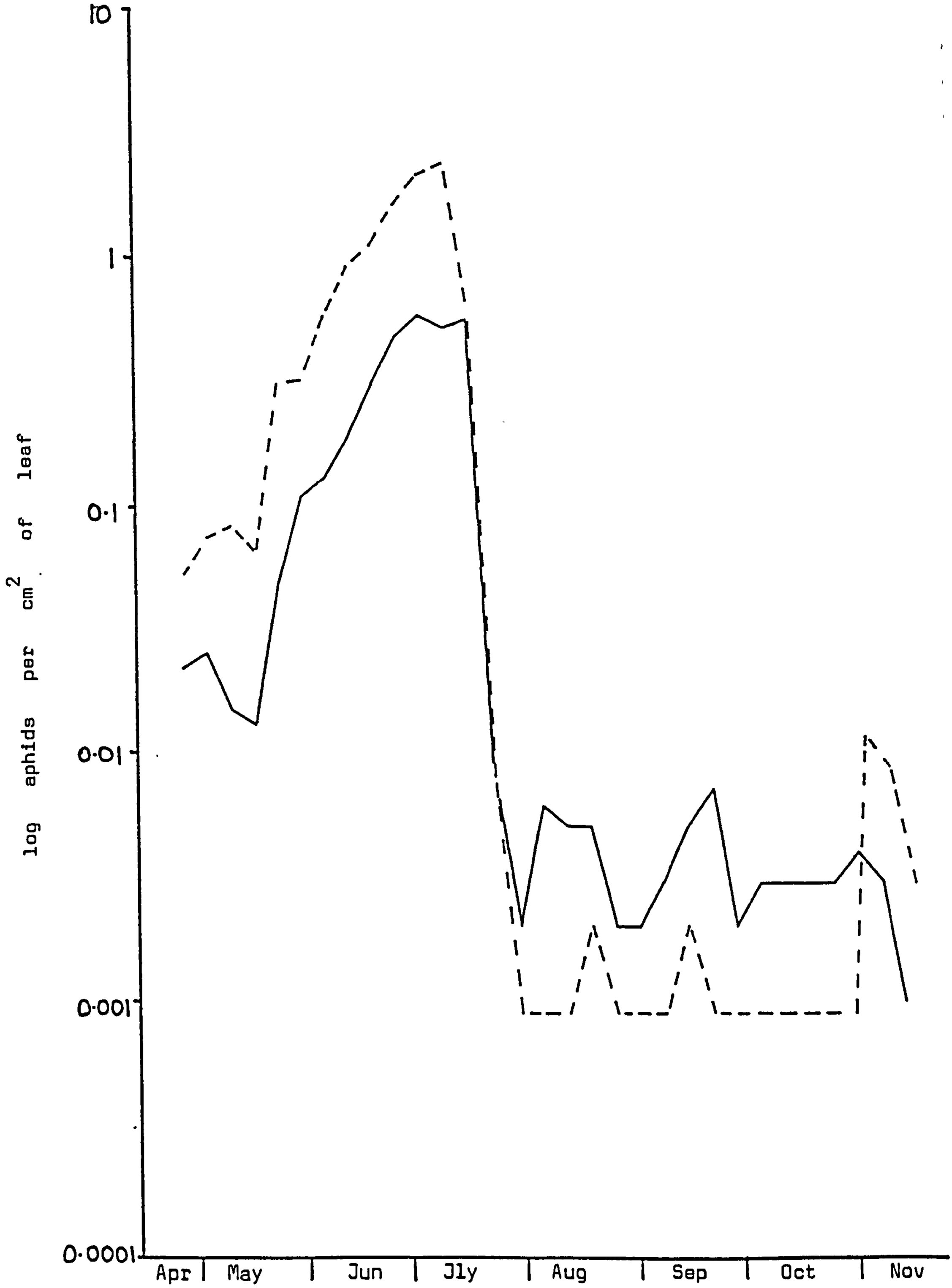


Figure 43 (a): Population density of P.alni on LF 125 (section 1) 1983

- - - Terminal leaves —— Non-terminal leaves

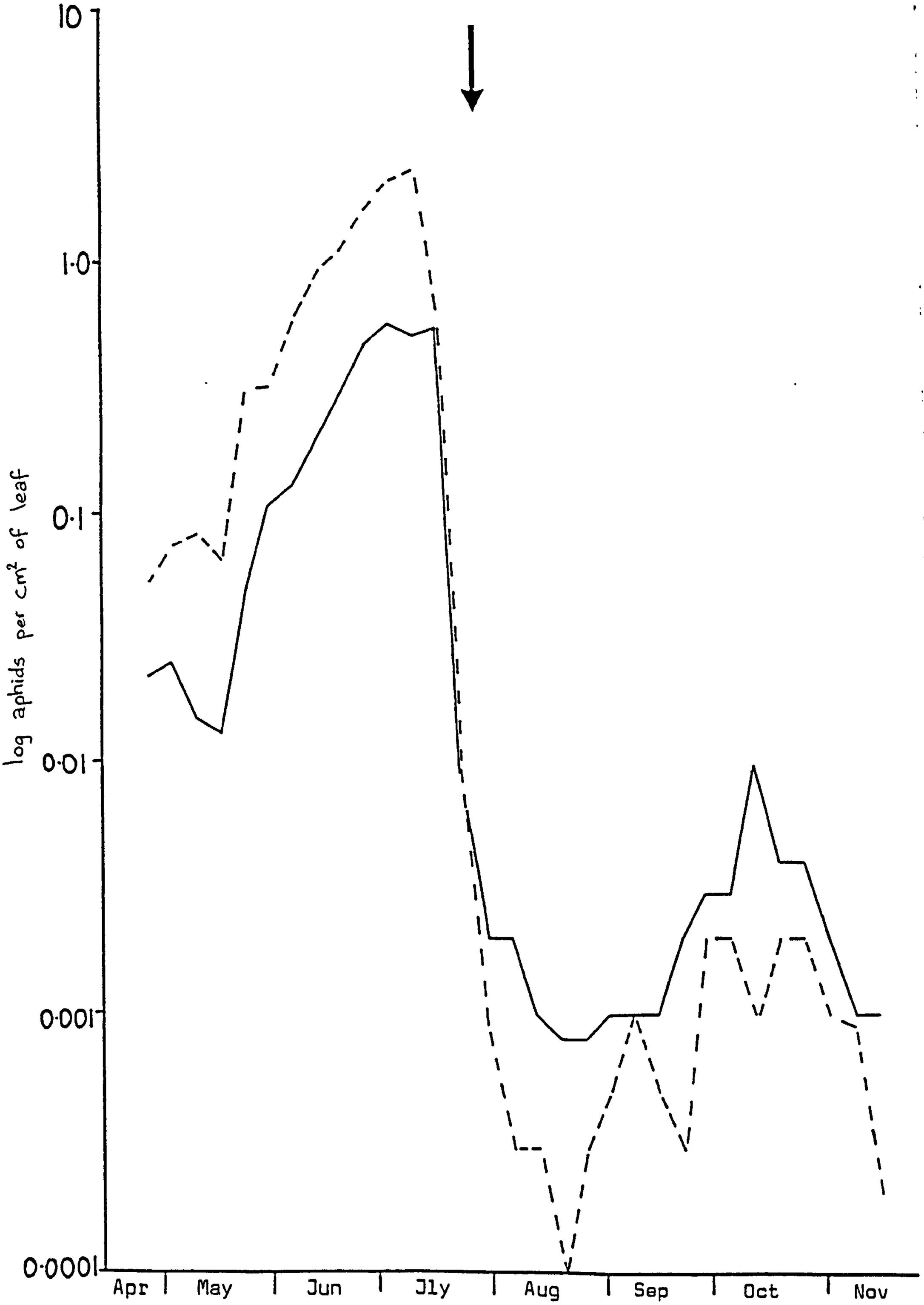


Figure 43 (b): Population density of P.alni on LF 125 (section 2) 1983. Arrow = pruning date.

– – – – – Terminal leaves ———— Non-terminal leaves

The age structures of the populations are depicted in fig.44 a and b. During the period of population growth instars I-III accounted for 70-90% of the population. When numbers declined this figure fell considerably with a greater proportion of adults appearing. The apterous fundatrices gave rise to a generation consisting of apterous and alate adults. The third and fourth generations appeared to be entirely alate whilst the fifth and sixth were apterous. The final generation of the year was the sexual form and thus P.alni had seven generations here in 1983.

There were differences between the age structure of the population on terminal leaves and that on non terminals (appendix 2.2). During the period of population growth fourth instars (presumptive alatae) formed a greater part of the population on terminals than on non terminals. This was reversed for alate adults; the proportion of these was higher on non terminals. At the time of the population peak and during the period of rapid decline instars I-III formed a greater proportion of the population on terminal leaves than on non terminals. Alatae first appeared in early June. The proportion of alate individuals in the fourth instar rose rapidly and by early July had reached 100% on both sections (fig.45).

Sexual forms appeared from mid October onwards. Males were only found on the pruned section during the second half of October. Oviparae were found on both sections from mid October until the end of November (fig.46a,c) and numbers were similar on each section (fig.46b,d).

(ii) Spatial distribution of aphids

On the unpruned section the value of b was 1.51 for terminals and 1.56 for non terminals. On the pruned section these values were 1.50 and 1.54 respectively (table 26). These values are significantly different from unity indicating that the aphids were aggregated over the whole season. The weekly values of Morisita's index were high to begin with,

Figure 44 (a) :

Age structure of the population on LF 125,

section 1, 1983.

(a) Alate adults

(b) Fourths (presumptive alatae)

(c) Apterous adults

(d) Fourths (presumptive apterae)

(e) Nymphs

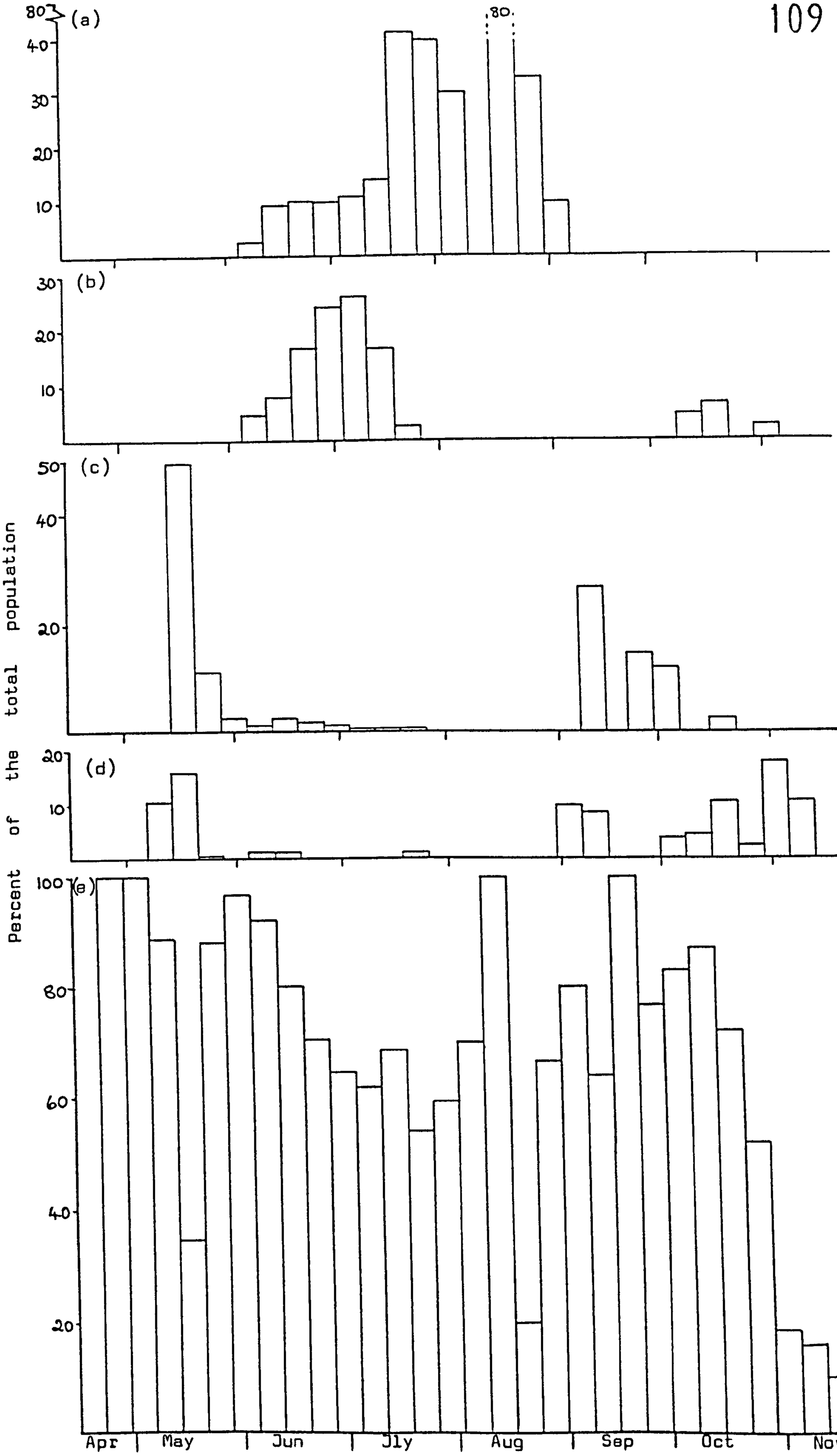

(a)
80
40
30
20
10
80
(b)
30
20
10
(c)
50
40
20
total population
(d)
20
10
Percent of the
(e)
100
80
60
40
20
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 44 (b):

Age structure of the population on LF 125,

section 2, 1983

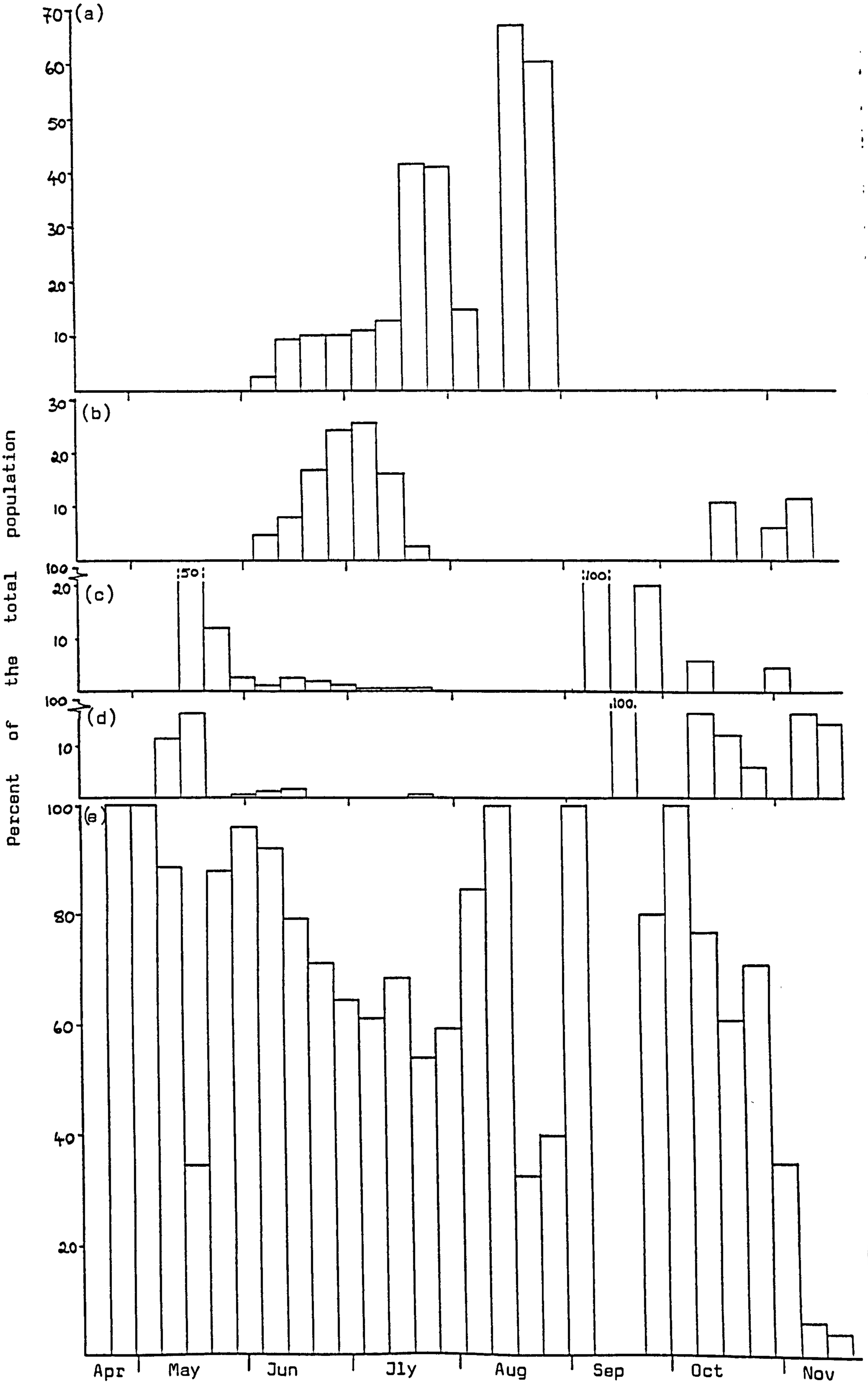
(a) Alate adults

(b) Fourths (presumptive alatae)

(c) Apterous adults

(d) Fourths (presumptive apterae)

(e) Nymphs


(a)
70
60
50
40
30
20
10
(b)
30
20
10
(c)
100
20
10
50
100
(d)
100
10
100.
(e)
100
80
60
40
20
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov
Percent of the total population

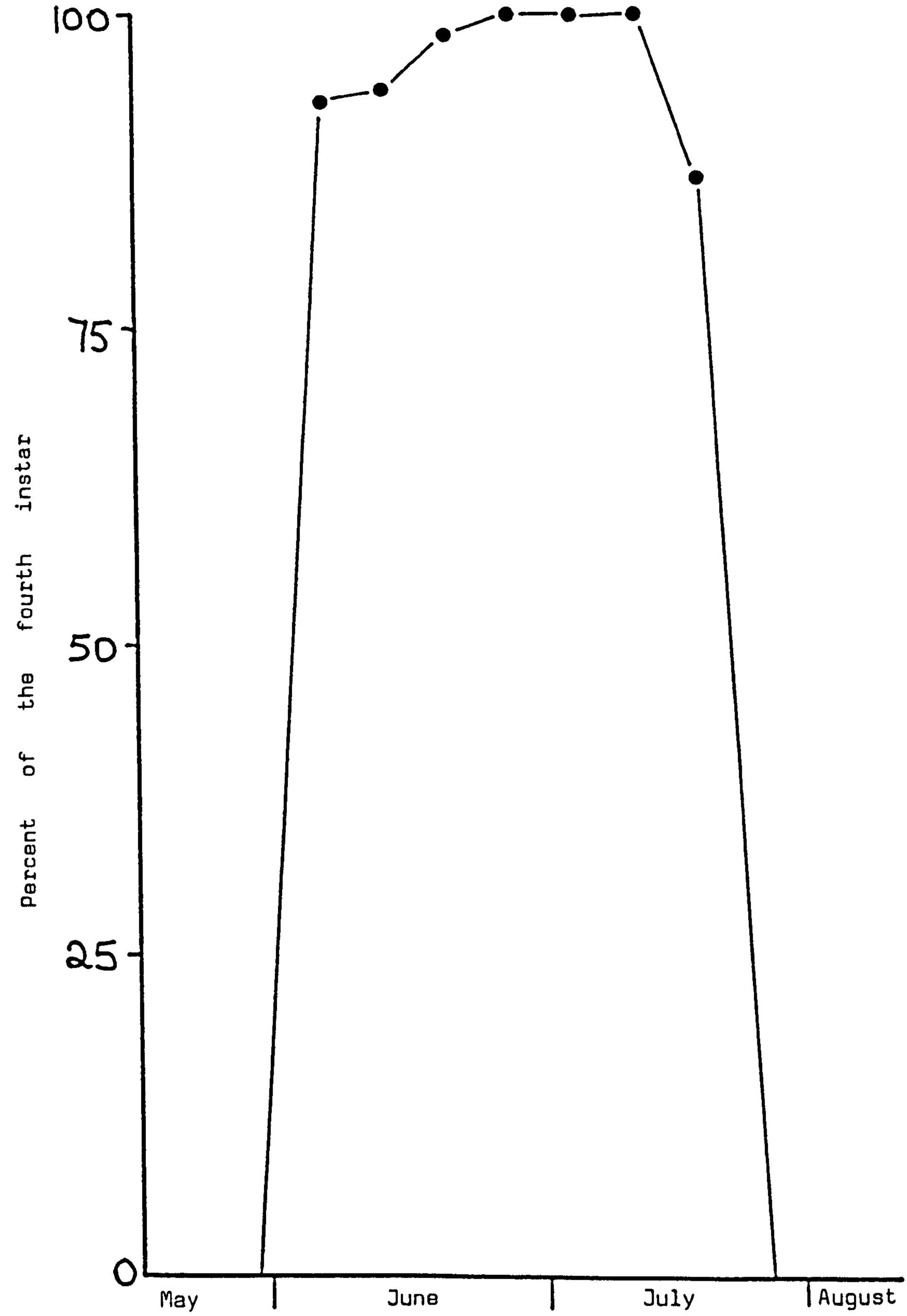


Figure 45: Proportion of presumptive alatae in the fourth instar, LF 125, 1983.

Figure 46:

Abundance of sexuales, LF 125, 1983

(a) Appearance of sexuales, section 1

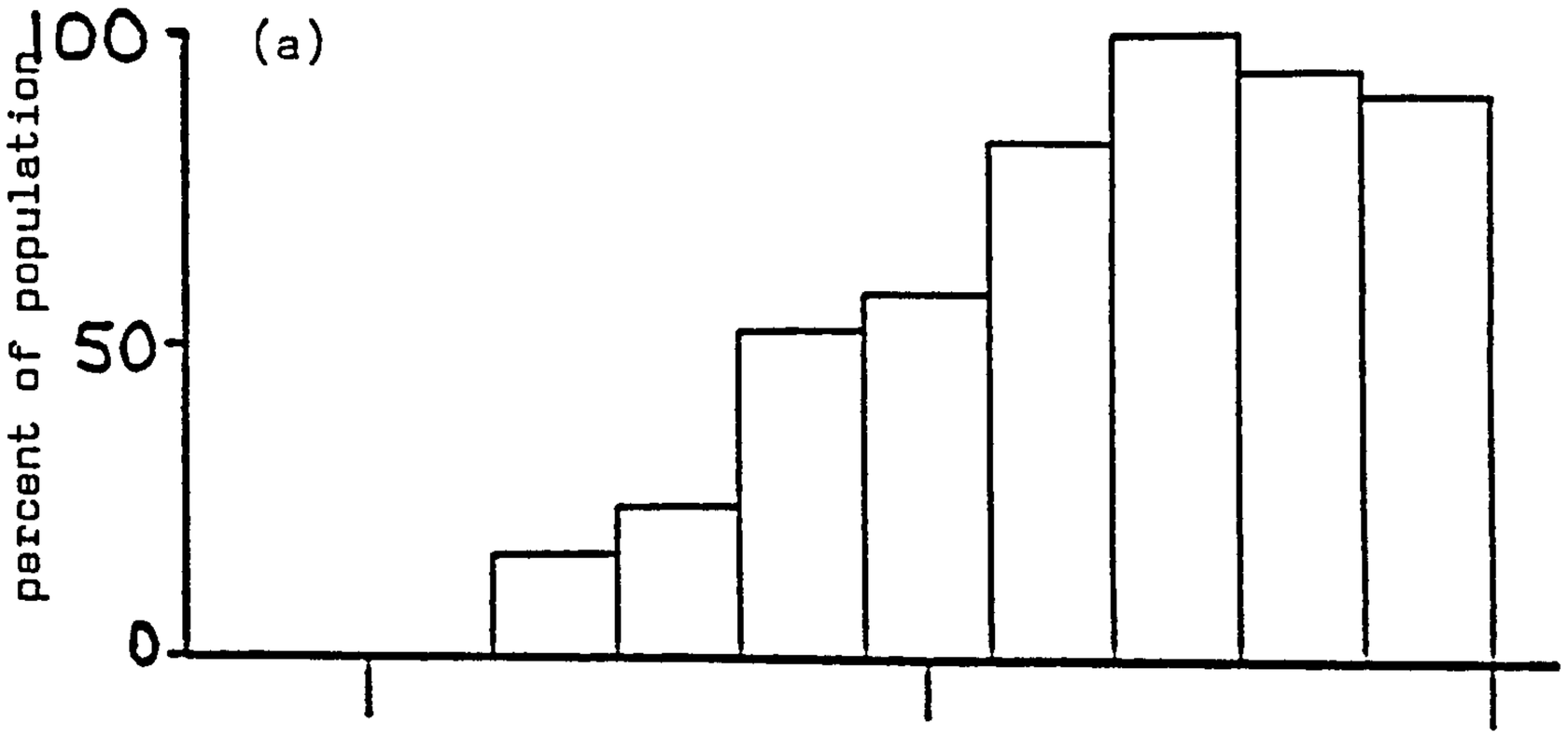
(b) Abundance of oviparae,section 1

(c) Appearance of sexuales, section 2

(d) Abundance of oviparae, section

males

oviparae


(a)
100
50
0
percent of population
(b)
15
6
0
oviparae/200 leaves
(c)
100
50
0
percent of population
(d)
8
4
0
oviparae/200 leaves
Sep
October
November

caused by aggregation of aphids when the eggs hatched. It fell as the aphids dispersed over the leaves but rose again when the fundatrices began reproducing. It then gradually fell as the population increased and more leaves were colonized (table 11). After the period of decline, when aphid numbers were at a low level the index assumed high values. Those aphids present were distributed as an 'adult plus offspring' on a few leaves. These gradually dispersed and the value became zero as the aphids present were distributed one to a leaf. Higher values were obtained in late autumn as oviparae congregated on the remaining available leaves.

(iii) Abundance of natural enemies

Predators were more abundant throughout the season than in 1982 (fig.47a,c). The ratio of predators to aphids was low during the period of aphid population growth. When aphid numbers were at a maximum there were 2 predators to every 1000 aphids present. However as the aphid population sharply declined, the ratio increased and in early August and early September there were three predators recorded to every aphid found on the unpruned section and six to every aphid on the pruned section. Pruning did not appear to have as great an effect on predator numbers as it did on the aphids, hence the extreme value of the ratio on the pruned section (fig.47 b,d). In addition to A.bipunctata, two other coccinellids were found, these being C.septempunctata and Psyllobora 22-punctata L. A.nemorum was again more abundant than A.nemoralis. Adult coccinellids and anthocorids appeared in mid May, having overwintered as adults. Coccinellids comprised about 3% of predators found on the windbreak and anthocorids 4%. As in 1982 mirids formed the greater part of predators recorded and the commonest was B.angulatus. This bug formed 68% of predator numbers on the unpruned section and 74% on the pruned section (fig.48a,b). Nymphs first appeared in mid June and adults were noted from mid July onwards. Numbers rapidly declined on each section as the

Table 11 MORISITA'S INDEX OF DISPERSION - LF125, 1983

Date		S E C T I O N 1		S E C T I O N 2	
		Terminal leaves	Non-terminals	Terminal leaves	Non-terminals
April	25	7.1	3.6	6.5	4.4
May	2	2.0	6.9	4.3	5.3
	9	4.3	3.6	5.2	4.4
	16	4.6	5.8	5.0	4.8
	23	9.6	6.9	8.4	5.7
	30	5.6	6.5	4.8	5.9
June	6	5.2	6.4	5.2	5.8
	13	4.5	6.3	3.4	4.9
	20	3.9	4.0	3.5	4.2
	27	2.8	2.6	2.4	2.7
July	4	2.9	2.5	2.1	2.4
	11	2.6	2.4	2.0	2.0
	18	3.0	1.8	2.4	2.1
	25	41.7	3.1	0	7.2
Aug	1		2.6	0	16.7
	8		16.7	0	
	15		33.3		0
	22	100.0	33.3	0	10.0
	29		0	0	32.1
Sept	5		0	0	19.1
	12		0	0	0
	19	0	33.3	0	16.7
	26		0	19.1	22.1
Oct	3	0	4.5	28.6	4.8
	10		8.5	10.0	24.7
	17		5.9	40.0	2.3
	24		2.9	20.0	8.0
	31		6.6	0	0
Nov	7	0	4.8	0	0
	14	18.7	8.4	0	0
	21	13.3	0	0	0
	25	0	4.8		

Figure 47:

Abundance of predators, LF 125,1983:

(a) Total number of predators, section 1

(b) Ratio of predators to aphids, section 1

(c) Total number of predators, section 2

(d) Ratio of predators to aphids, section 2

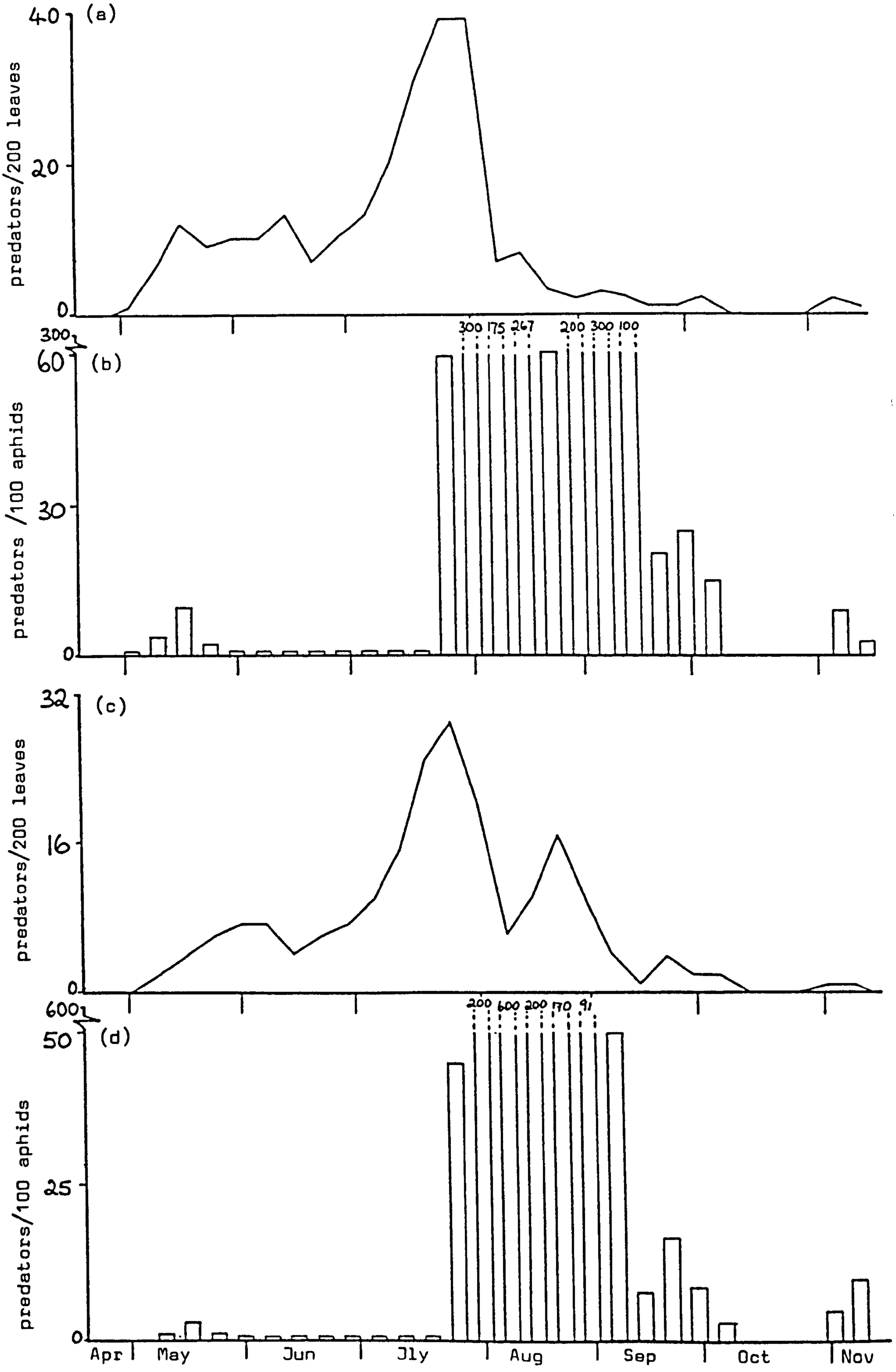

(a)
40
20
0
predators/200 leaves
(b)
300
60
30
0
predators /100 aphids
300 175 267 200 300 100
(c)
32
16
0
predators/200 leaves
(d)
600
50
25
0
predators/100 aphids
200 600 200 170 91
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 48:

Relative abundance of predators by classes,

LF 125, 1983

(a) Section 1

(b) Section 2

(1) Coccinellidae

(2) Anthocoridae

(3) B.angulatus

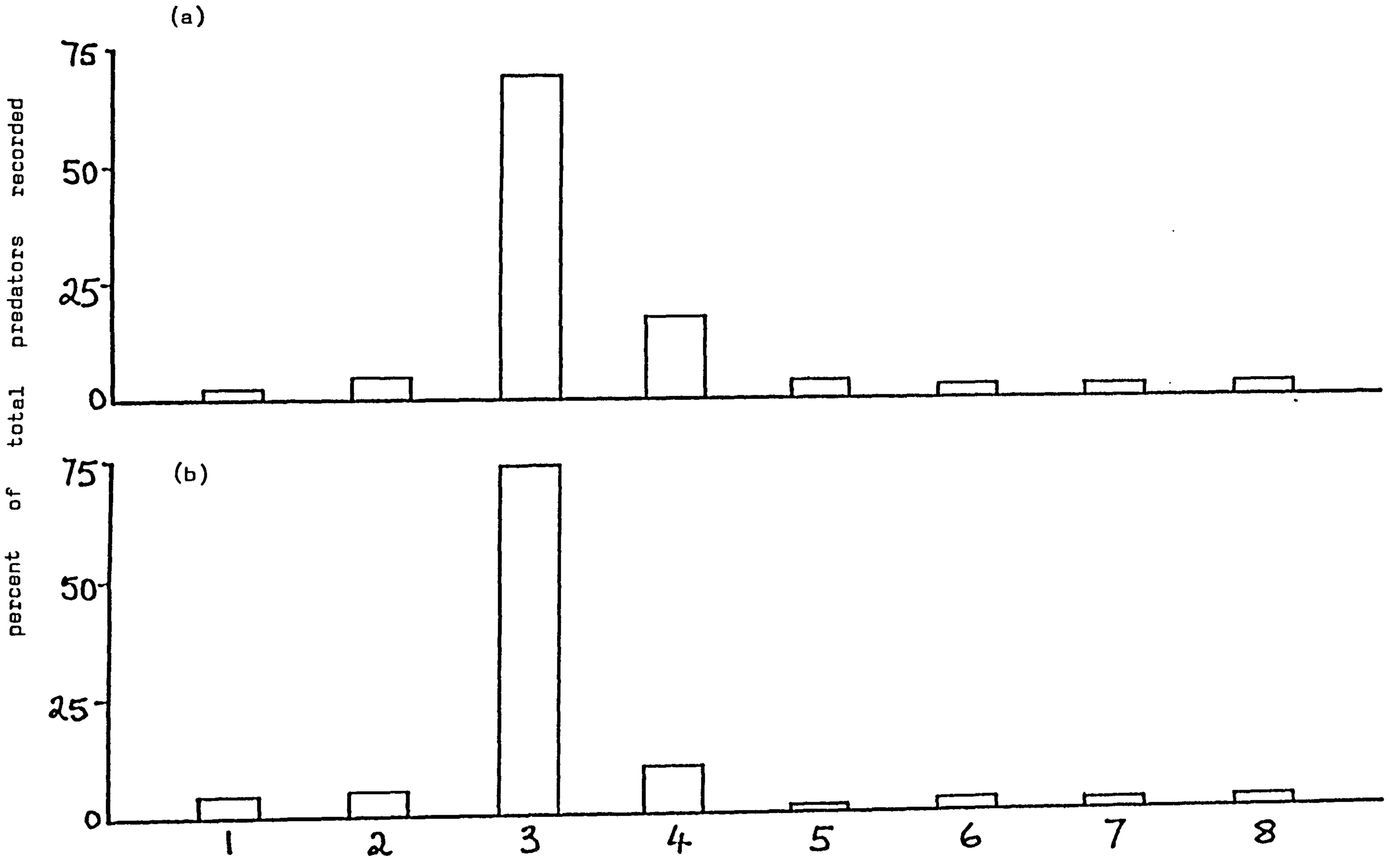
(4) O.marginalis

(5) P.ambiguus

(6) Neuroptera

(7) Syrphidae

(8) Cecidomyiidae


(a)
75
50
25
0
percent of total predators recorded
(b)
75
50
25
0
1
2
3
4
5
6
7
8

bugs became adult, a likely reason being emigration from the windbreak as soon as the bugs were able to fly, due to the lack of aphid prey at this time (fig.49a,b). O.marginalis preceded B.angulatus in its appearance, nymphs being present from mid May and adults from late June. It was the second commonest predator, comprising 17% of total numbers on the unpruned section and 10% on the pruned section (fig.48). P.ambiguus appeared in small numbers as did larvae of the cecidomyiid, A.aphidimyza. Amongst the neuroptera, C.carnea was found occasionally and also adult specimens of Hemerobius humulinus L. Larvae of the syrphids Syrphus ribesii L. and Episyrphus balteatus Degeer were found during July.

Parasitism first occurred in mid June and continued until mid October. Aphids were parasitized by T.pallidus but mummified carcasses caused by by Praon spp were also found. The extent of parasitism was similar on both sections, being about 11% at the peak level in early July (fig.50 a.b.)

Isolated examples of aphids killed by the fungus Entomophthora occidentalis Humber (Waterhouse and Brady,1982) were found during August (fig.50).

(iv) LF126 1983

As in 1982 no aphids were found on A.cordata or A.incana during the early part of the season. The first aphids recorded were alates in late June. Populations increased rapidly as more alates appeared and began reproducing. The decline in numbers was equally rapid and by early August no aphids were found (figs.51 and 52). Alate adults formed a considerable proportion of the population throughout (figs.53 and 54) and some of the offspring produced matured as apterous adults.

The only predators recorded were adult B.angulatus which appeard at the same time as their numbers declined on LF125, suggesting that they had arrived from that windbreak. Numbers were low and coincided with the

Figure 49:

Abundance of B.angulatus on LF 125 during 1983

(a) Section 1

(b) Section 2

Nymphs

Males

Females

Figure 50:

Parasitism and fungal disease in populations of P.alni on LF 125, 1983

(a) Section 1

(b) Section 2

——— parasitism

– – – Entomophthora

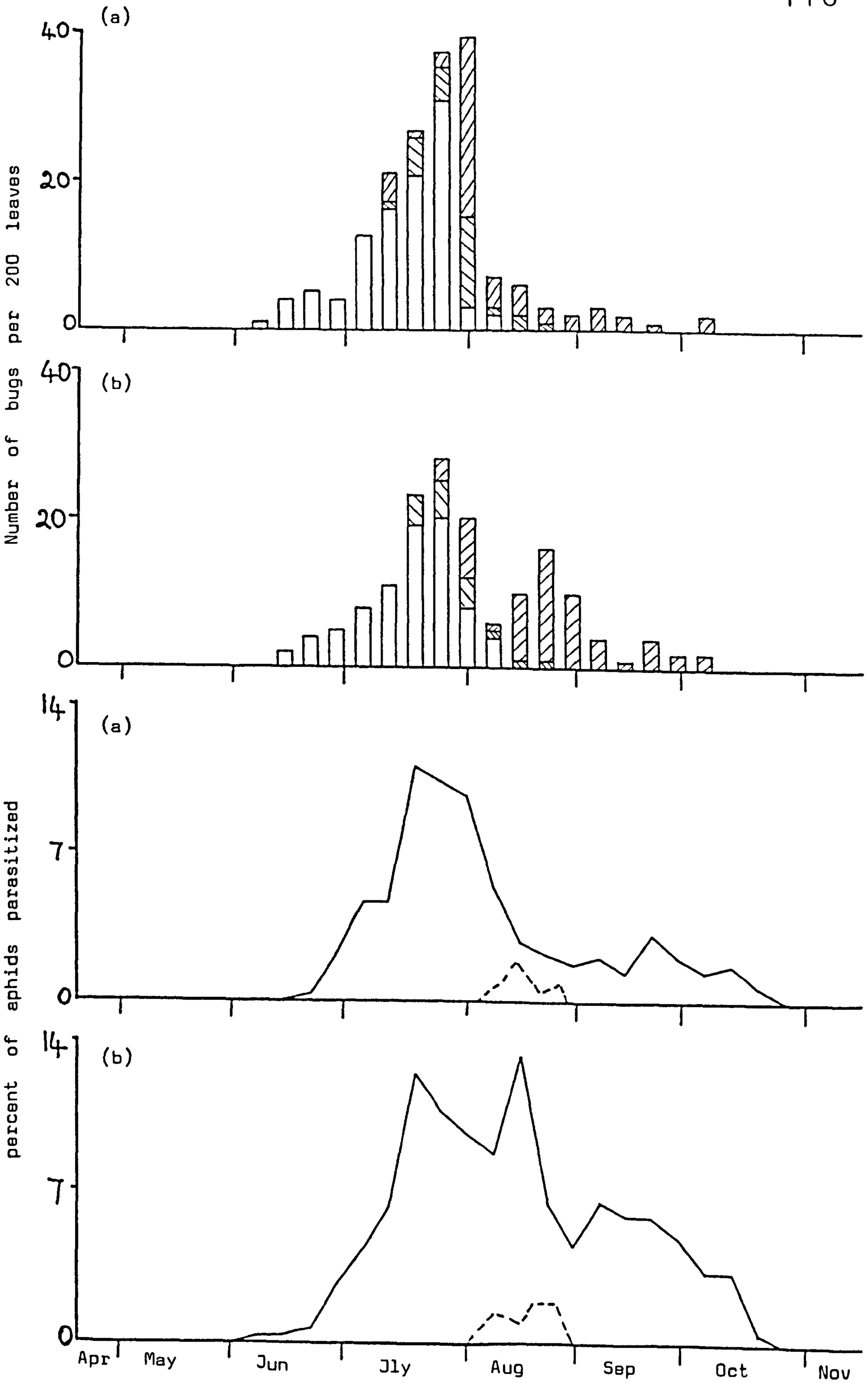

(a)
40
20
0
per 200 leaves
(b)
40
20
0
Number of bugs
(a)
14
7
0
percent of aphids parasitized
(b)
14
7
0
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 51:

Abundance of aphids on LF 126, A.incana 1983:

(a) per 100 leaf sample

- - - Terminal leaves

——— Non-terminal leaves

(b) per 200 leaf sample

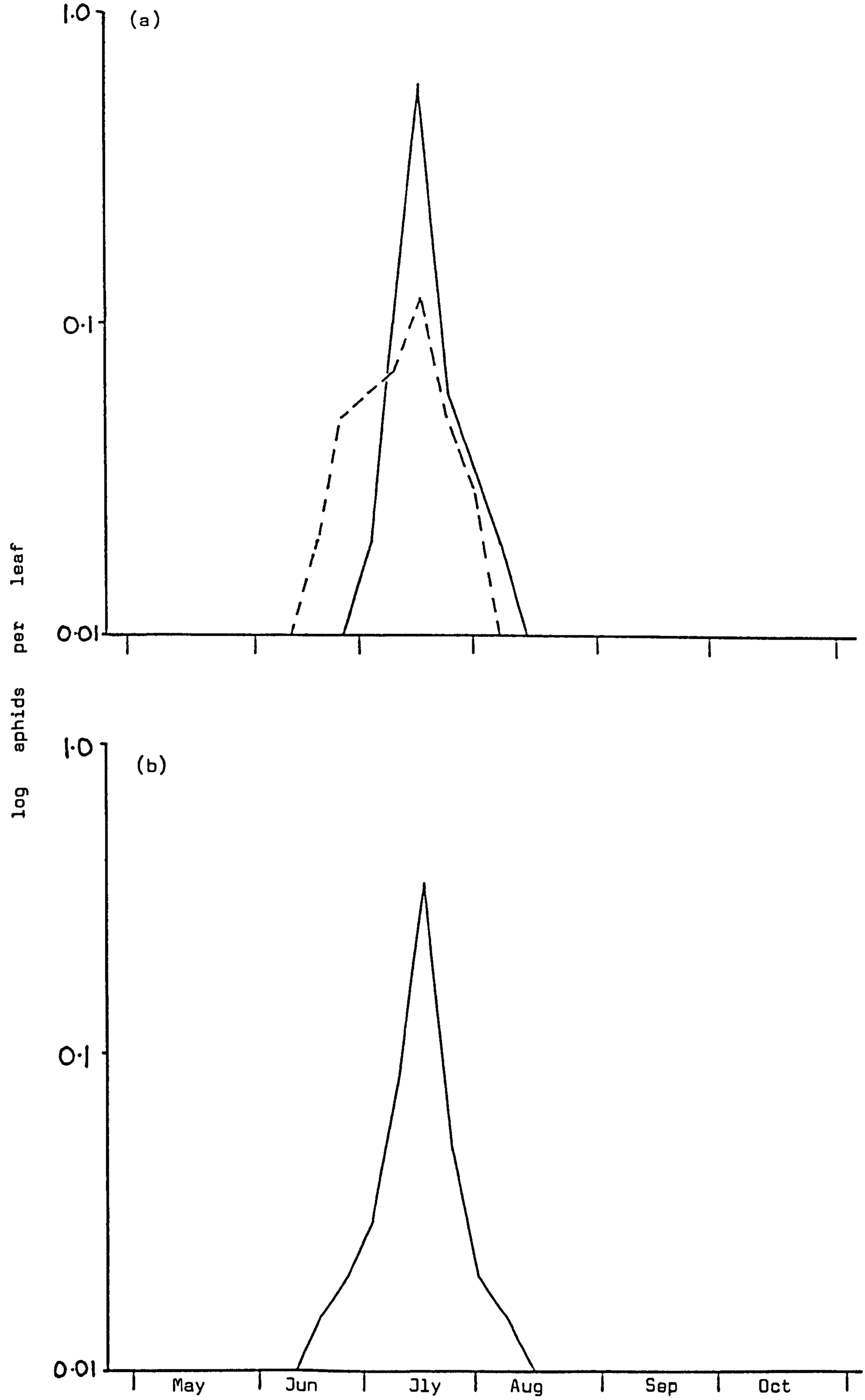

(a)
1·0
0·1
0·01
log aphids per leaf
(b)
1·0
0·1
0·01
May
Jun
Jly
Aug
Sep
Oct

Figure 52

Abundance of aphids on LF 126, A.cordata 1983

(a) per 100 leaf sample

- - - Terminal leaves

——— Non-terminal leaves

(b) per 200 leaf sample

(a)

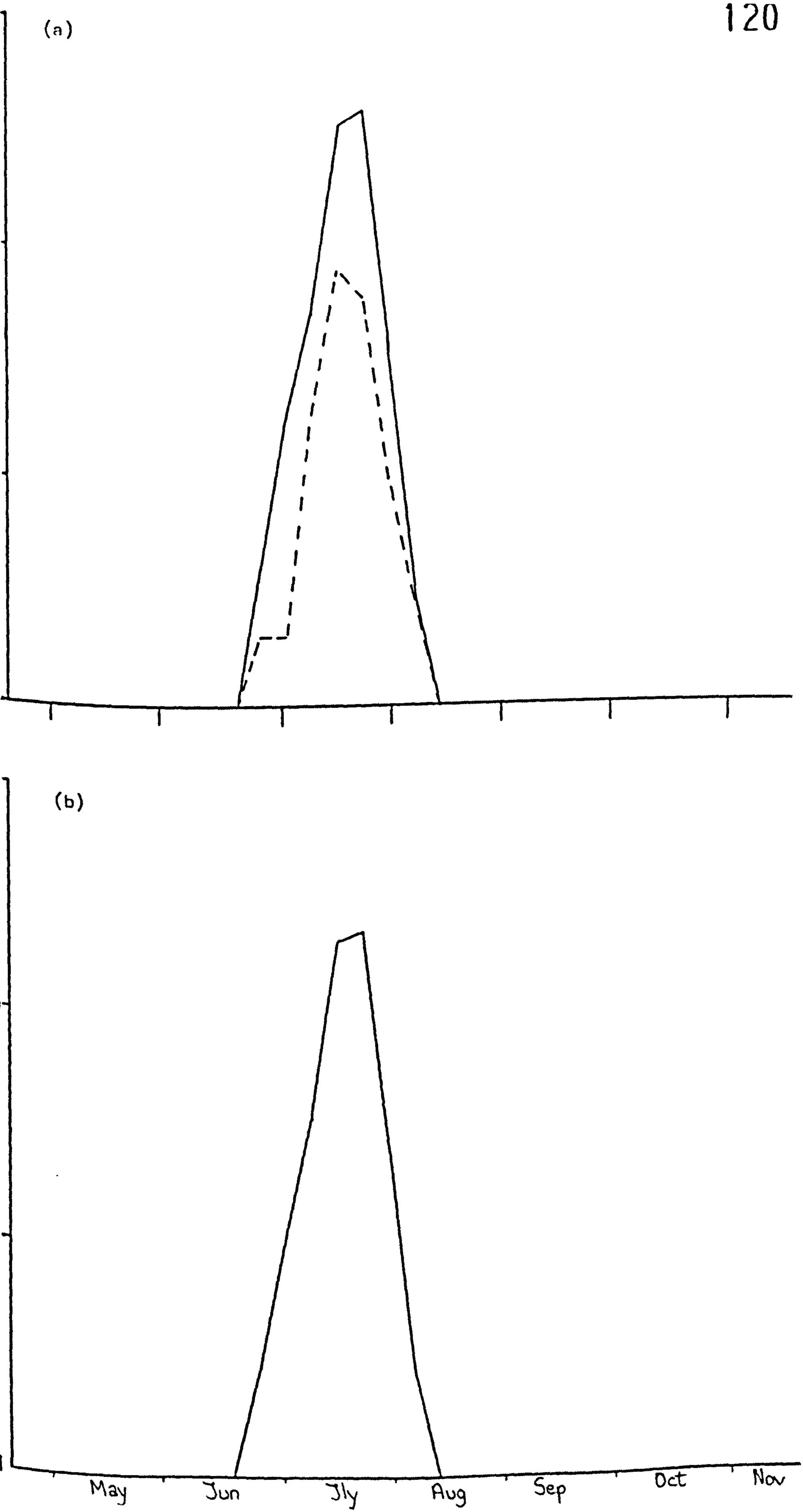

10
1·0
0·1
0·01
log. aphids per leaf
(b)
10
1·0
0·1
0·01
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 53:

Age structure of the population on LF 126, A.incana,1983

(a) Alate adults

(b) Apterous adults

(c) Nymphs

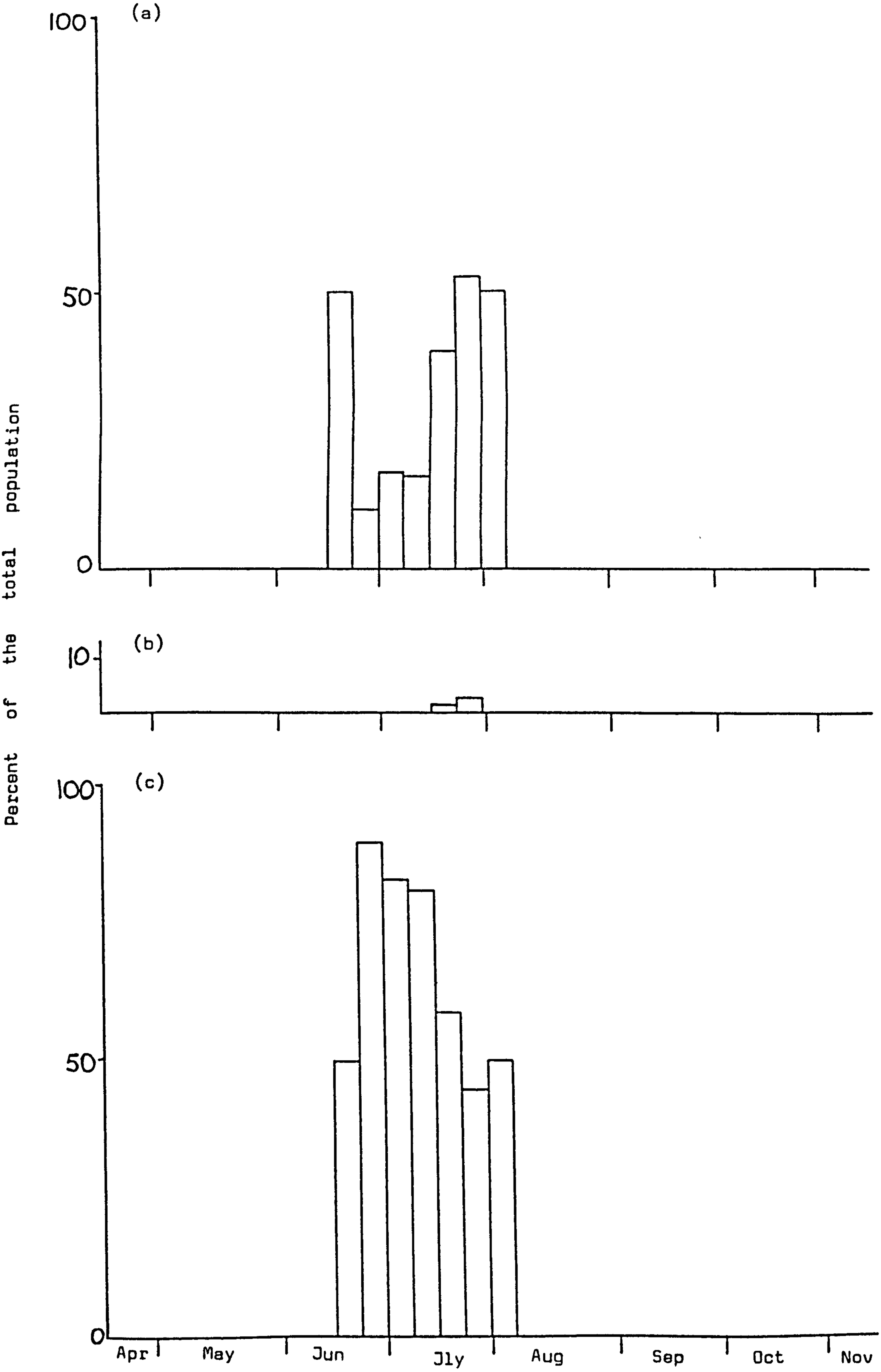

(a)
100
50
0
(b)
10
(c)
100
50
0
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

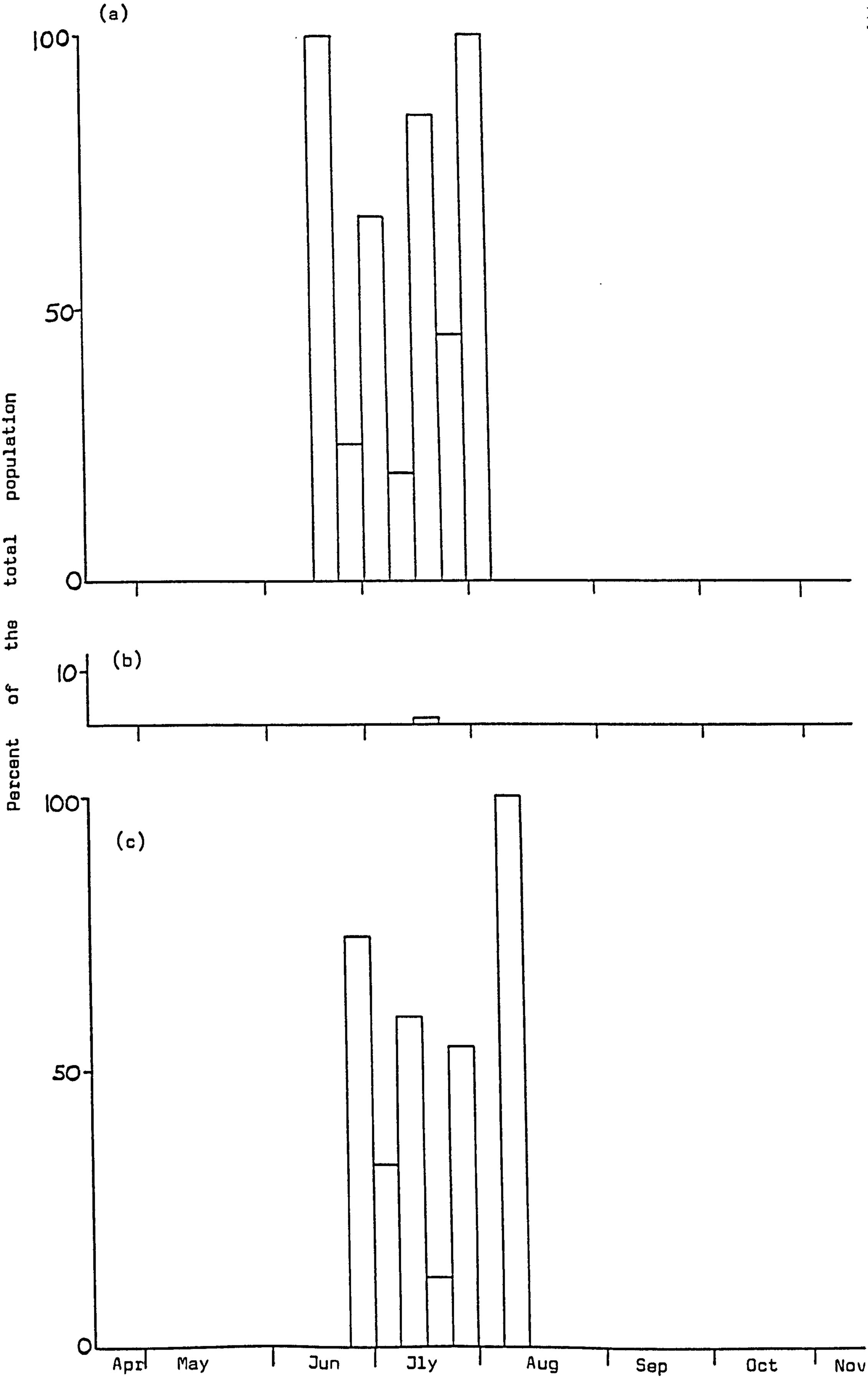
Figure 54:

Age structure of the population on LF 126, A.cordata,1983

(a) Alate adults

(b) Apterous adults

(c) Nymphs


(a)
100
50
0
(b)
10
(c)
100
50
0
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

disappearance of aphids on LF126.

2.5.3. LF125 and LF126, 1984

(i) Abundance of aphids

The section of windbreak which was not pruned in summer 1983 was cut during the winter and left uncut during summer 1984. The other section was left during the winter and cut between July 30th and August 7th 1984. Aphids hatched from eggs in late April at a similar time to those in 1982 and 1983. Initial numbers of fundatrices on both sections were considerably less than in 1983. Populations increased and peak numbers were reached in mid July, on the same day each section (figs.55a, 56a). Following peak numbers the populations declined sharply with small resurgences in late summer (table 12).

On both sections the pattern of abundance on terminal and non terminal leaves was fairly similar and that on non terminals was closest to the total population (figs.55b,56b). The aphid density was greatest on terminal leaves throughout most of the period of population build-up but later in the season when leaf growth ceased on the unpruned section and after pruning on the other section, this trend tended to be reversed (fig.57a and b).

Analysis of the age structure of the populations (figs.58 and 59) indicates that throughout the period of build up of numbers instars I-III accounted for 70-90% of the population. This figure fell during July and August when numbers were very low but rose again in September when populations appeared to consist only of nymphs. The apterous fundatrices gave rise to a second generation which was almost entirely apterous. The third and fourth generations were almost entirely alatiform, the fifth generation mostly apterous and the sixth generation entirely so. The sexual forms were the seventh and last generation.

Figure 55:

Aphid abundance on LF 125, section 1, 1984:

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

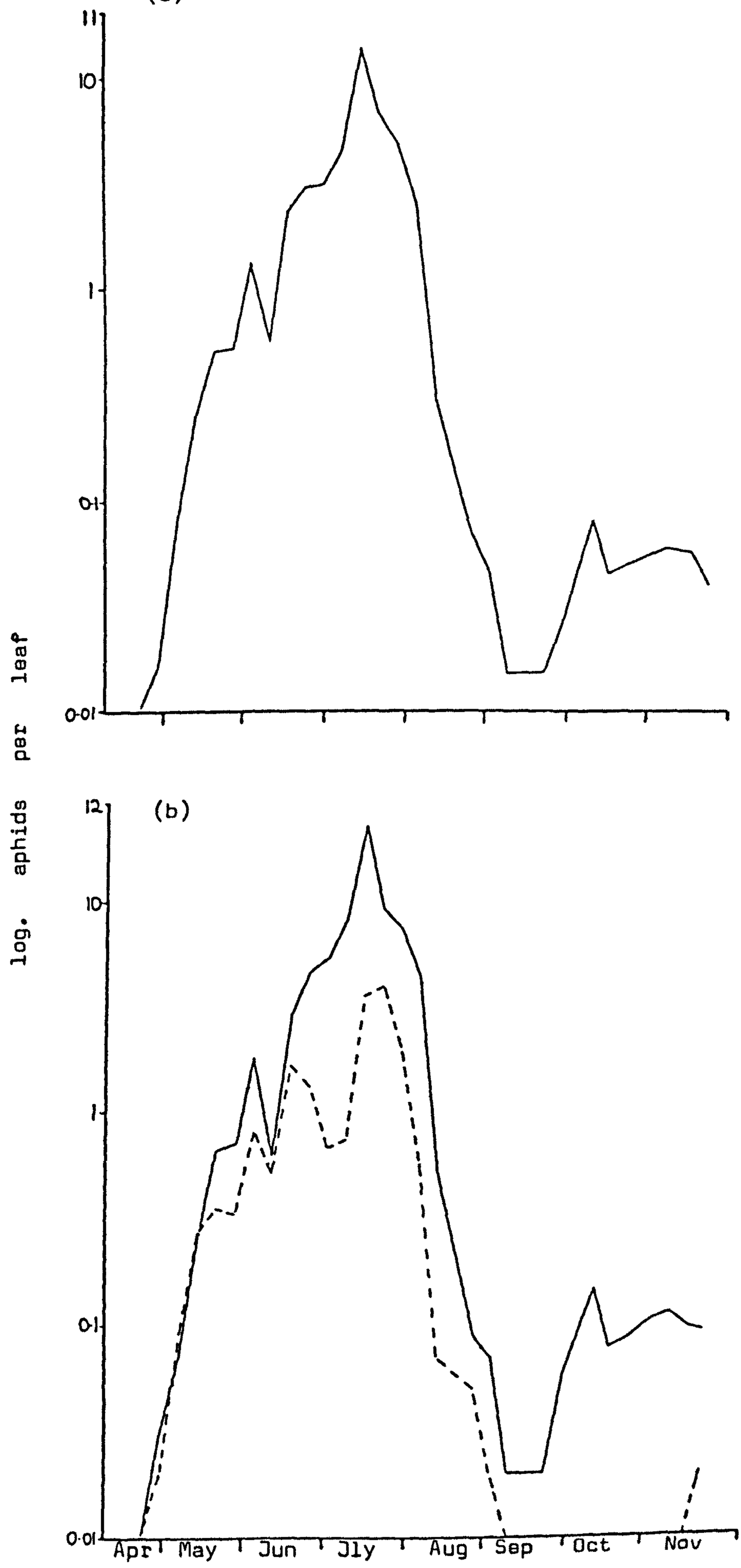

(a)
log. aphids per leaf
100
10
1
0·1
0·01
(b)
12
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 56:

Aphid abundance on LF 125, section 2,1984

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

Arros indicate date of pruning

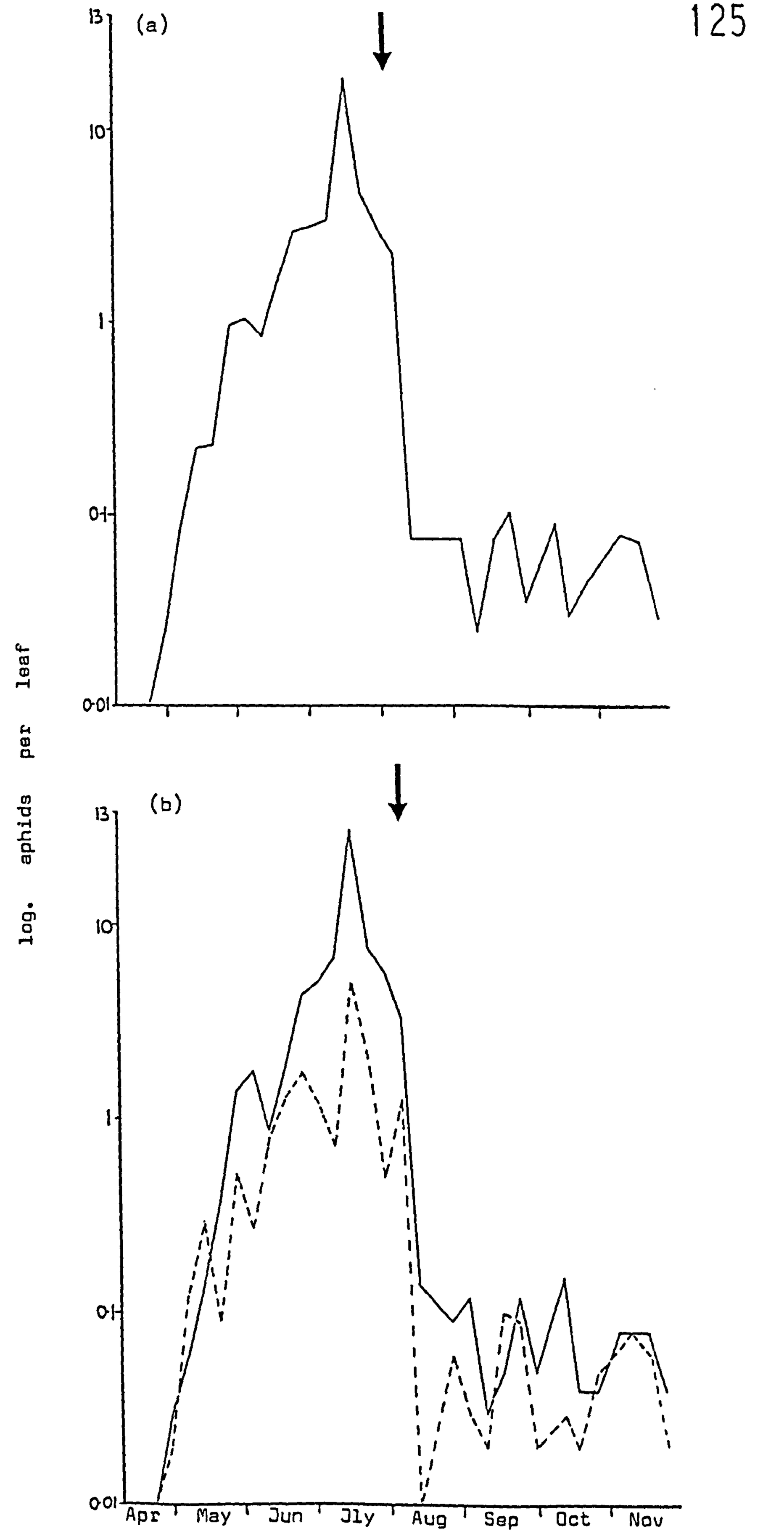

(a)
13
10
1
0·1
0·01
log. aphids per leaf
(b)
13
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Table 12 TOTAL NUMBER OF APHIDS IN LEAF SAMPLES - LF125, 1984

Date		S E C T I O N 1			S E C T I O N 2		
		Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample	Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample
April	30	1	2	3	1	2	3
May	7	8	6	14	11	5	16
	14	26	25	51	29	13	42
	21	34	65	99	7	37	44
	28	32	70	102	51	139	190
June	4	81	180	261	27	174	201
	11	51	61	112	79	87	166
	18	166	290	456	130	198	328
	25	131	463	594	171	426	597
July	2	68	538	606	120	506	620
	9	74	827	901	72	675	747
	16	354	2371	2725	498	3250	3748
	23	396	935	1331	203	763	966
	30	201	749	950	49	577	626
Aug	7	59	437	496	126	328	454
	13	6	53	59	0	13	13
	27	4	8	12	5	8	13
Sept	3	1	6	7	2	11	13
	10	0	1	1	1	2	3
	17	0	1	1	9	4	13
	24	0	1	1	8	11	19
Oct	1	0	5	5	1	4	5
	12	0	14	14	2	14	6
	18	0	17	17	1	3	4
	26	0	8	8	4	3	7
Nov	9	0	10	10	7	7	14

Figure 57:

Population density of P.alni on LF 125, 1984

(a) Section 1

(b) Section 2

- - - Terminal leaves

——— Non-terminal leaves

Arrow represents pruning date

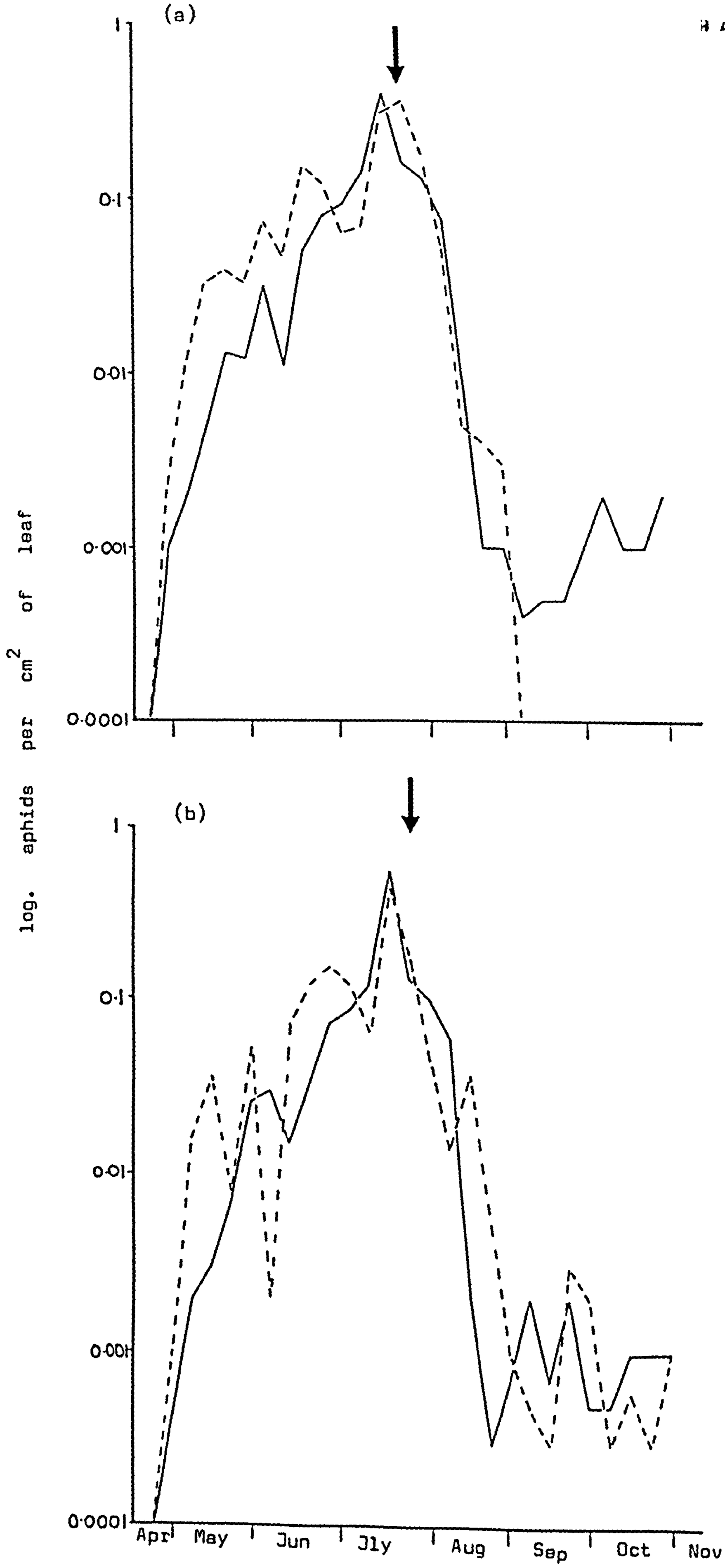

(a)
1
0·1
0·01
0·001
0·0001
log. aphids per cm² of leaf
(b)
1
0·1
0·01
0·001
0·0001
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 58:

Age structure of the population on LF 125,

section 1, 1984

(i) Alate adults

(ii) Fourths (presumptive alatae)

(iii) Apterous adults

(iv) Fourths (presumptive apterae)

(v) Nymphs

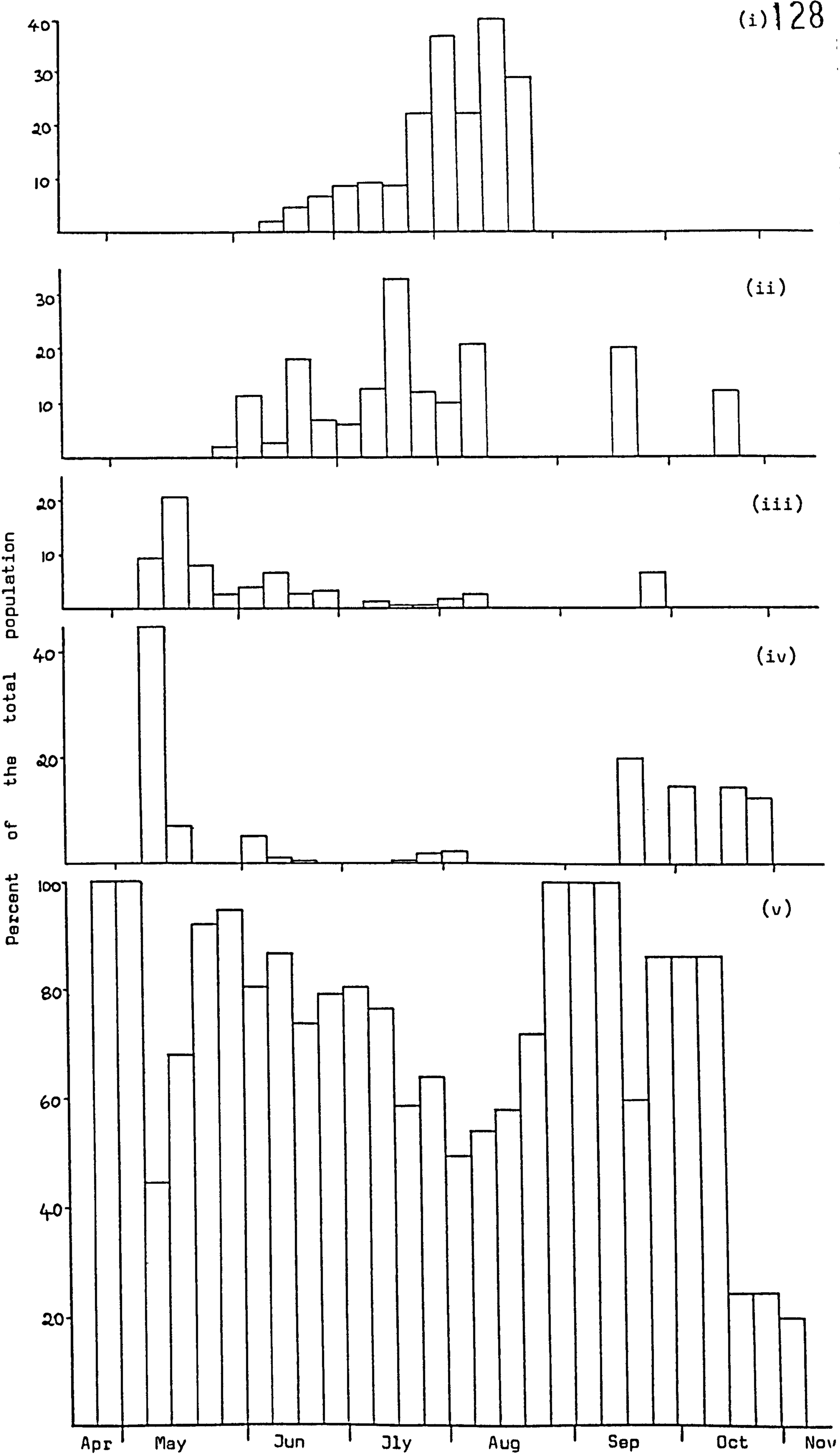
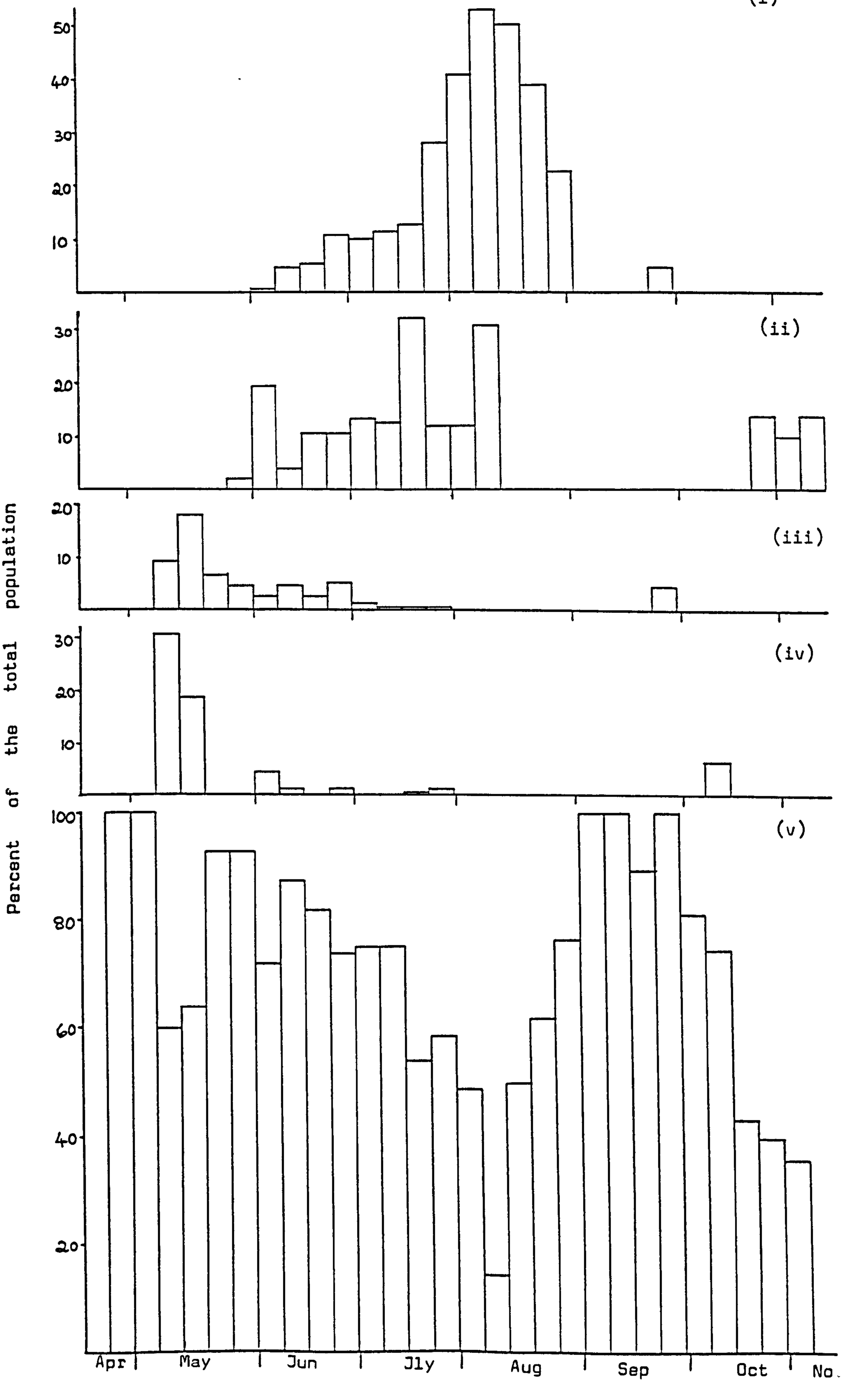

(i)
40
30
20
10
(ii)
30
20
10
(iii)
20
10
(iv)
40
20
(v)
100
80
60
40
20
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 59:

Age structure of the population on LF 125

section 2, 1984

Legend as for Figure 58.


(i)
50
40
30
20
10
(ii)
30
20
10
(iii)
20
10
population
(iv)
30
20
10
Percent of the total
(v)
100
80
60
40
20
Apr
May
Jun
Jly
Aug
Sep
Oct
No

The age structure of the populations on the terminal and non terminal leaves was fairly similar (appendix 2.3,2.4). There tended to be a greater proportion of alate adults on the non terminal leaves at the time of the population peak. Alate forms first appeared in mid June. Numbers rose rapidly and by mid July at the population peak the fourth instar consisted entirely of presumptive alatae (fig.60). Numbers subsequently declined and presumptive alatae were found until mid August. Sexual forms were present from mid October, males preceding the appearance of oviparae (fig61a,c). Numbers were similar on each section (fig.61b,d) and oviparae were present until late November.

(ii) Spatial distribution of aphids

On the unpruned section the value of b for terminal leaves was 1.55 and for non terminals 1.54. On the pruned section the values were 1.49 and 1.60 respectively (table 26). All these values are significantly different from unity indicating that the aphids were aggregated over the whole season. The weekly values of the Morisita index showed a very similar trend to those of 1983 (table 13). The values were high when the fundatrices began reproduction, showed a gradual decline during the period of population growth and attained high values late in the season as the population became 'patchy' with the reproduction by successive generations of viviparae.

(iii) Abundance of natural enemies

Predators were similar in numbers to those of 1983, with slightly more present on the unpruned section (fig.62a,c). The ratio of predators to aphids showed a similar trend to that of 1983 (fig.62b,d,). When aphid numbers were very low during early September the ratio reached very high values on the unpruned section. It rose from four predators per 1000 aphids at the aphid population peak to ten per aphid in early September. With fewer predators being present on the pruned section, the ratio rose to one per aphid.

Figure 60:

Proportion of presumptive alatae in the fourth instar, LF 125, 1983

(a) Section 1

(b) Section 2

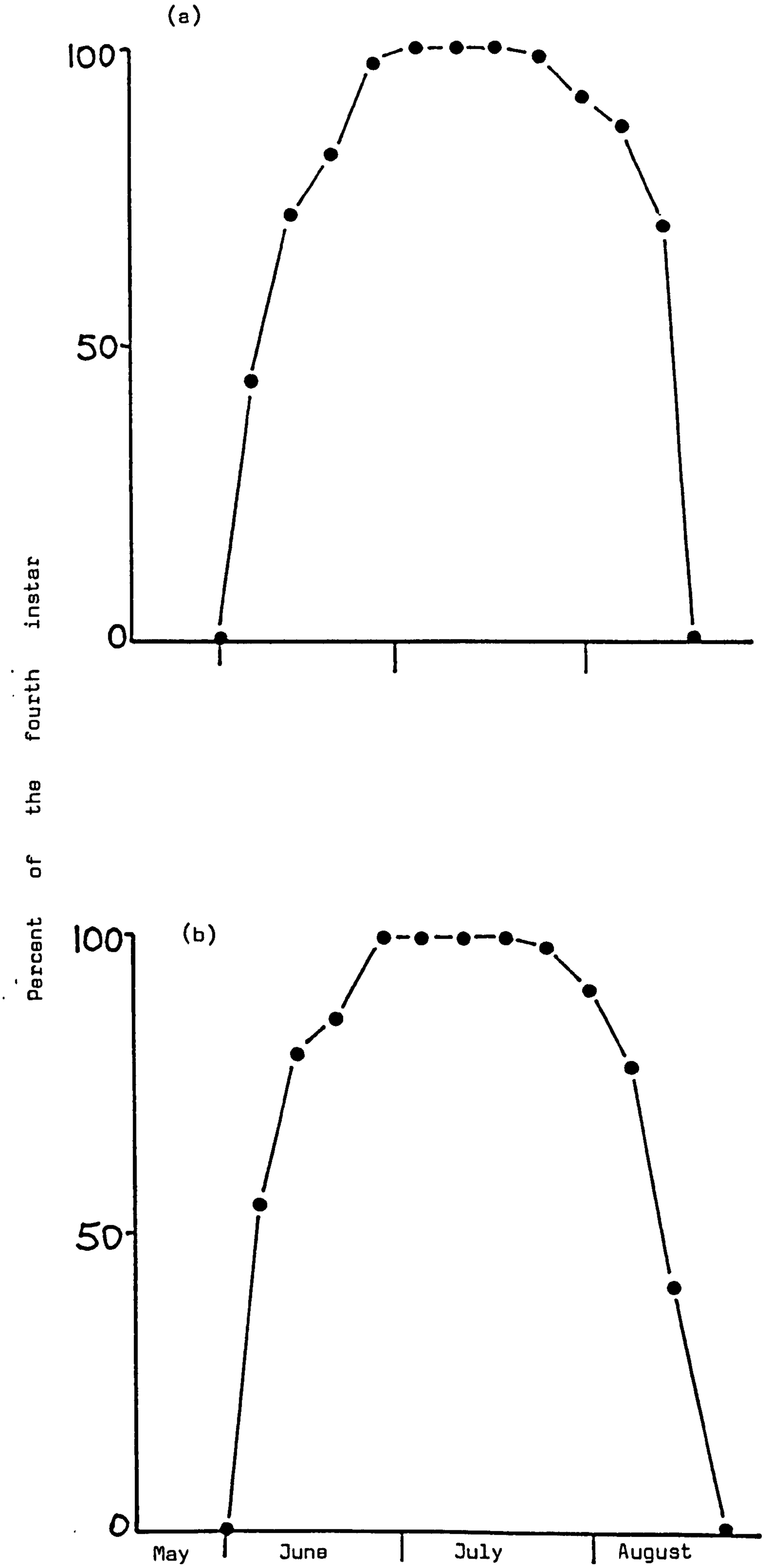

(a)
100
50
0
(b)
100
50
0
May
June
July
August
Percent of the fourth instar

Figure 61:

Abundance of sexuales, LF 125, 1984

(a) Appearance of sexuales,section 1

(b) Abundance of oviparae, section 1

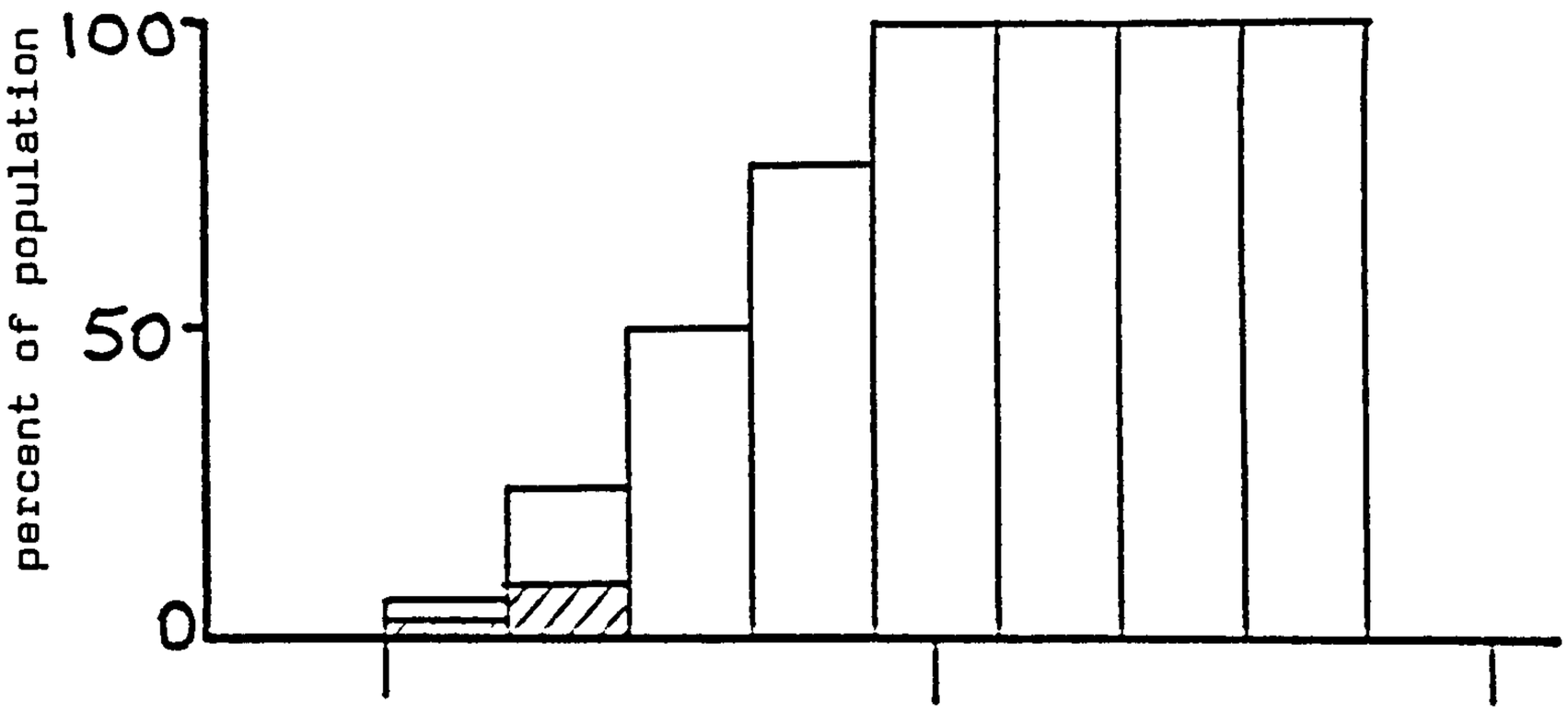
(c) Appearance of sexuales,section 2

(d) Abundance of oviparae, section 2

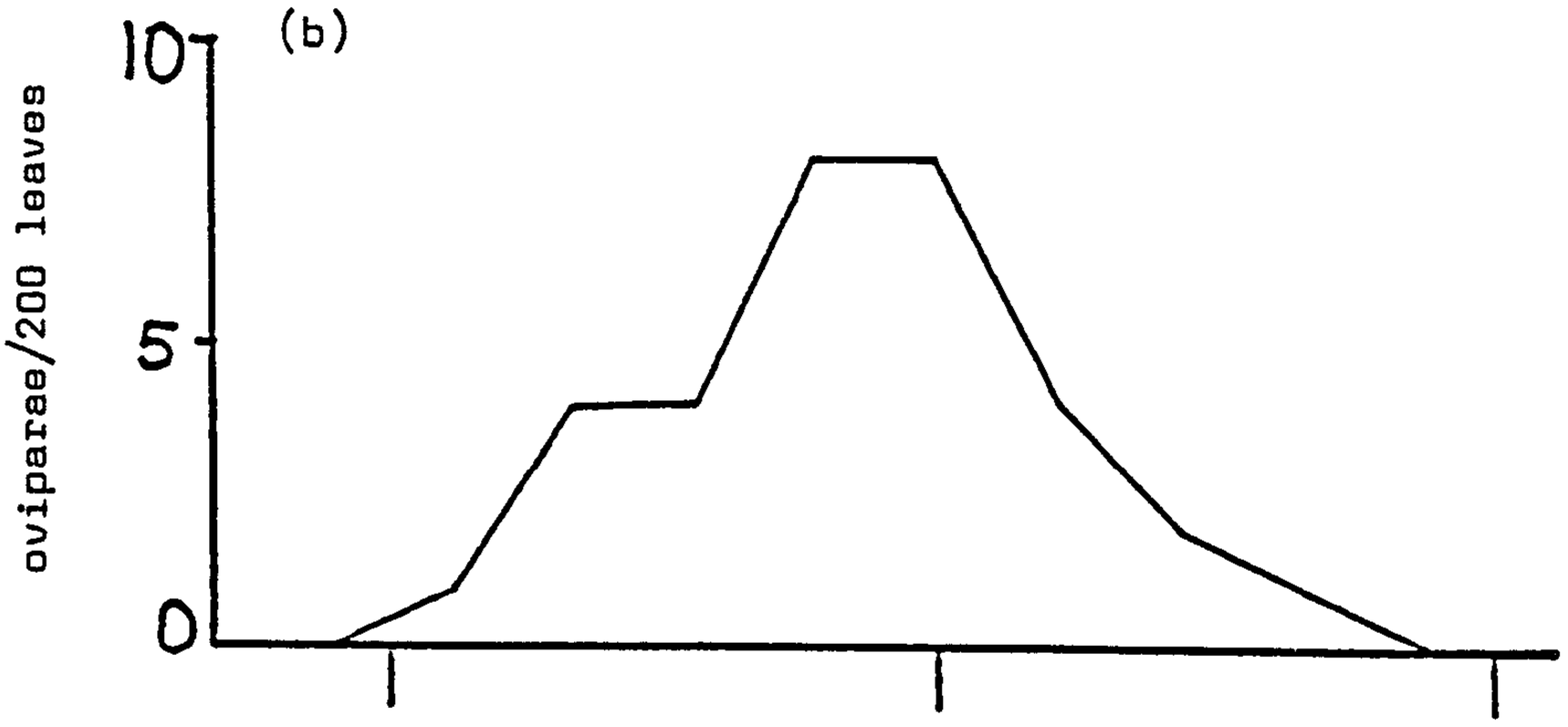
▨ males

□ oviparae

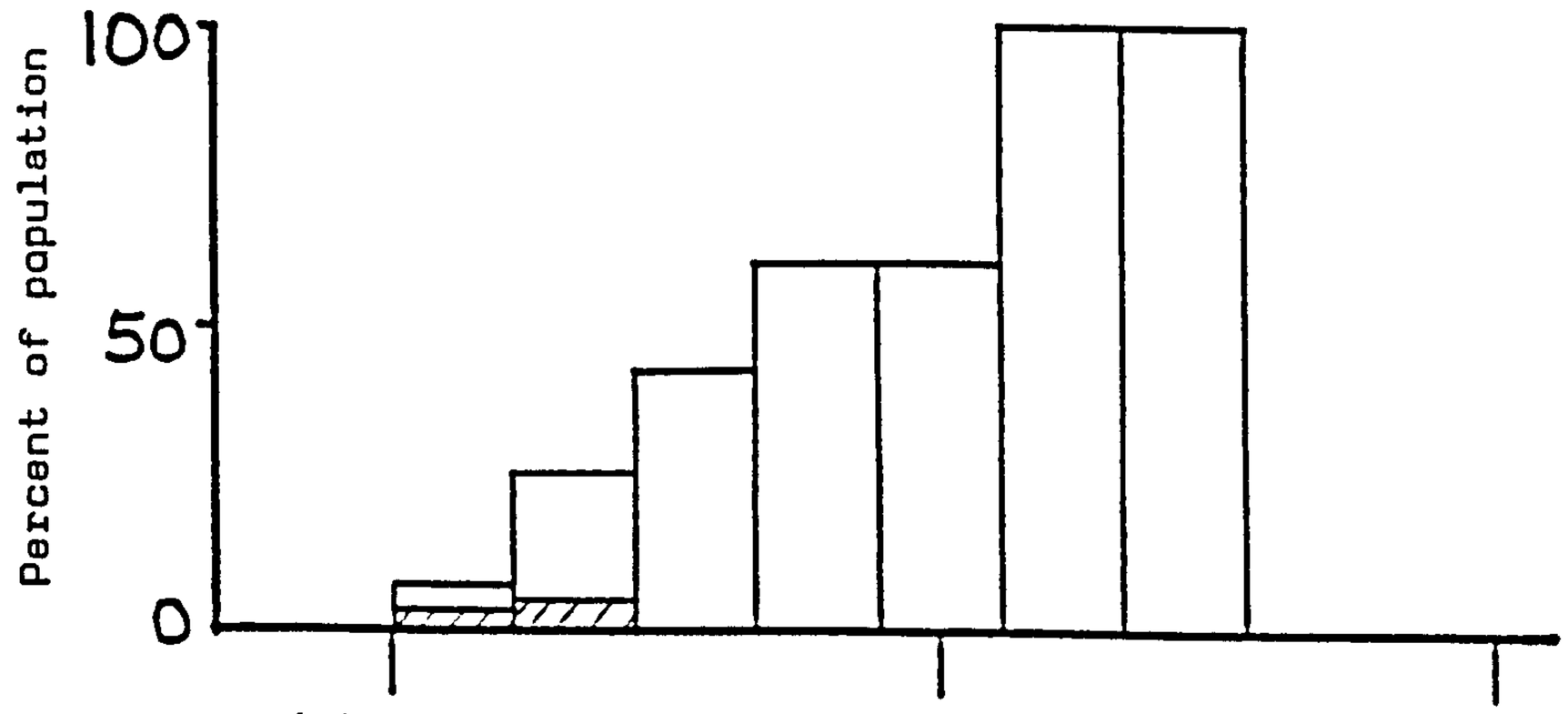
(a)


100
50
0
percent of population

(b)


10
5
0
oviparae/200 leaves

(c)


100
50
0
Percent of population

(d)

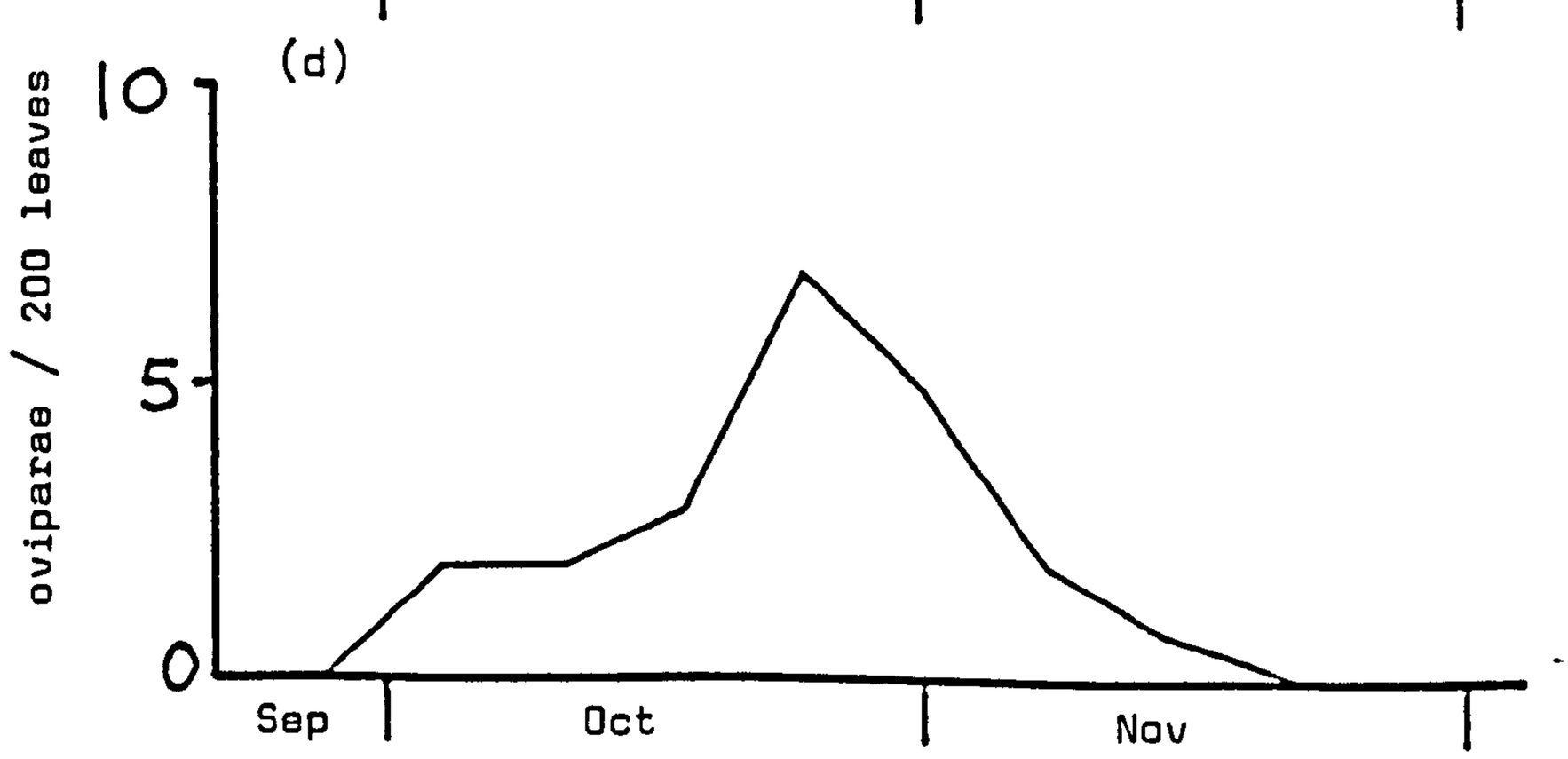

10
5
0
oviparae / 200 leaves
Sep
Oct
Nov

Table 13 MORISITA'S INDEX OF DISPERSION - LF125, 1984

Date		S E C T I O N 1		S E C T I O N 2	
		Terminal leaves	Non-terminals	Terminal leaves	Non-terminals
April	30	0	0	0	0
May	7				
	14	5.9	10.5	3.4	6.4
	21	20.5	18.8	4.8	13.7
	28	29.4	18.1	2.2	16.9
June	4	20.4	28.1	7.7	22.8
	11	12.9	13.6	8.7	6.8
	18	12.6	7.7	4.4	10.6
	25	4.2	5.5	6.1	3.1
July	2	6.3	5.7	7.7	6.9
	9	7.0	10.8	7.4	5.0
	16	7.0	2.5	5.8	5.5
	23	5.1	3.3	13.6	3.3
	30	9.3	2.0	6.7	2.7
Aug	7	3.3	2.5	4.4	3.0
	13	0	2.4		2.2
	27	0	3.6	20.0	3.6
Sept	3	0	6.7	0	3.6
	10		0	0	0
	17		0	16.7	0
	24		0	3.6	21.8
Oct	1		0	0	0
	12		28.6	0	25.0
	18		14.3	0	0
	26		3.6	16.7	0
Nov	9		13.3	19.1	41.6
	23			20.0	0

Figure 62:

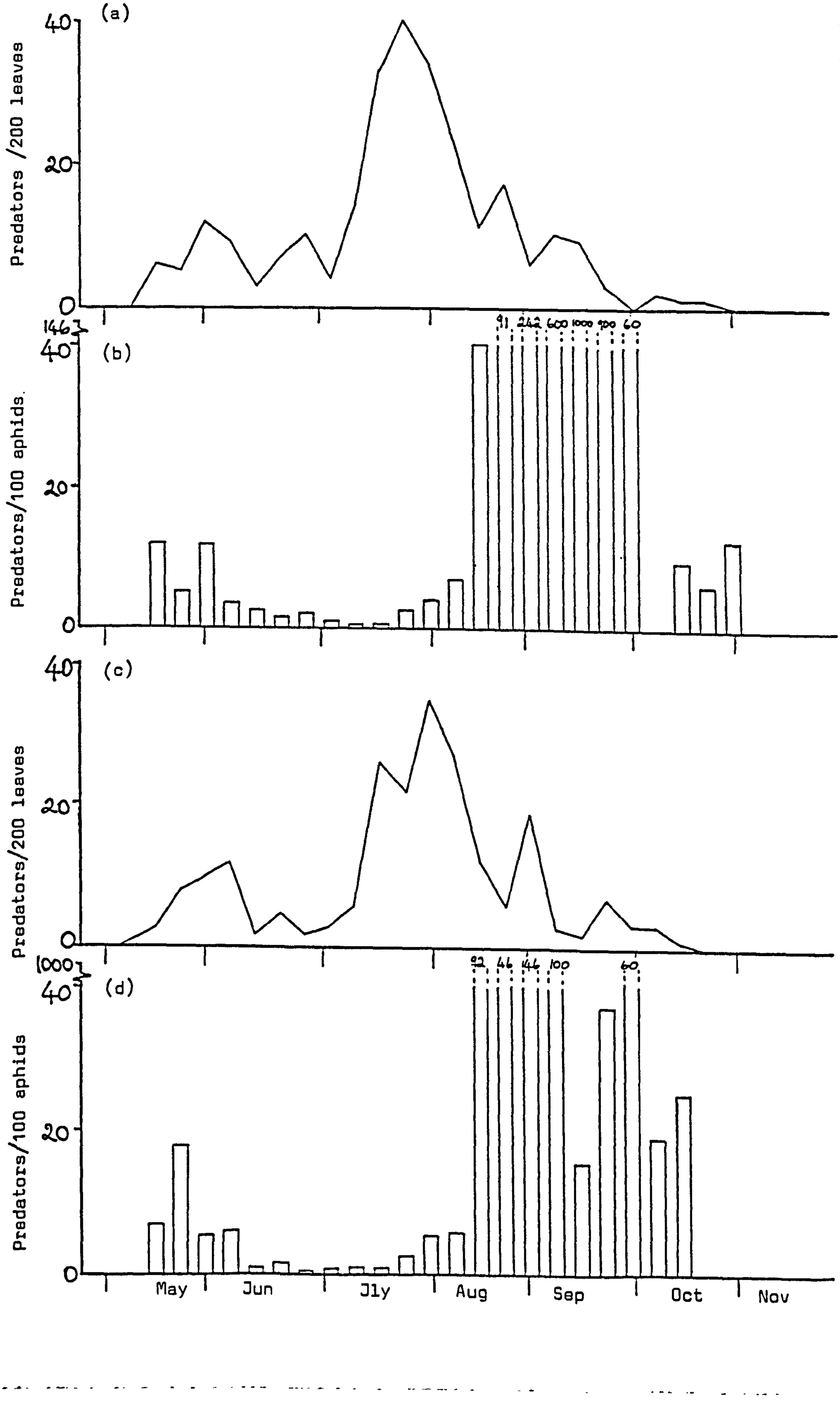
Abundance of predators, LF 125, 1984:

(a) Total number of predators, section 1

(b) Ratio of predators to aphids, section 1

(c) Total number of predators, section 2

(d) Ratio of predators to aphids, section 2


(a)
Predators /200 leaves
40
20
0
(b)
Predators/100 aphids
146
91 242 600 1000 900 60
40
20
0
(c)
Predators/200 leaves
40
20
0
(d)
Predators/100 aphids
1000
92 46 44 100 60
40
20
0
May
Jun
Jly
Aug
Sep
Oct
Nov

B.angulatus was again the commonest predator accounting for 74% and 73% on the pruned and unpruned sections respectively (fig.63). Nymphs first appeared in early July and adults from late July onwards (fig.64a,b). Again as in 1983 numbers declined as the bugs became adult, suggesting emigration from the windbreak. Other predators recorded were as for 1983. O.marginalis was again the second most common predator. Coccinellids accounted for 3% and anthocorids 4% of total numbers (fig.63).

Parasitism was less on the pruned section, reaching a peak of 9.3% compared with 12.8% on the unpruned section, but the difference was not significant ($d=0.898$, $p>0.05$). Parasitism occurred from late June until mid September, peak levels being recorded in mid July (fig.65a,b). Emerged wasps were all of T.pallidus and occasional Praon cocoons were found. No incidences of aphids killed by fungal disease were found.

(iv) LF126, 1984

As happened in 1982 and 1983 the first aphids found were alate adults. Their appearance in mid July coincided with their disappearance from LF125 at a similar time. Populations increased briefly but disappeared within a month (fig.66 a,b). Specimens of B.angulatus and one A.nemorum were found during August.

(v) Meteorological data

Temperature at East Malling was recorded as accumulated day degrees above $6^{o}C$. The weekly totals for the period April-October inclusive are shown in fig.67 for 1982, 83 and 84. It may be seen that the spring of 1982 was warmer than that of 1983 or 84. Temperatures were higher during summer 1983 and lowest during summer 1984.

Figure 63:

Relative abundance of predators by classes,

LF 125, 1984

(a) Section 1

(b) Section 2

(1) Coccinellidae

(2) Anthocoridae

(3) B.angulatus

(4) O,marginalis

(5) P.ambiguus

(6) Neuroptera

(7) Syrphidae

(8) Cecidomyiidae

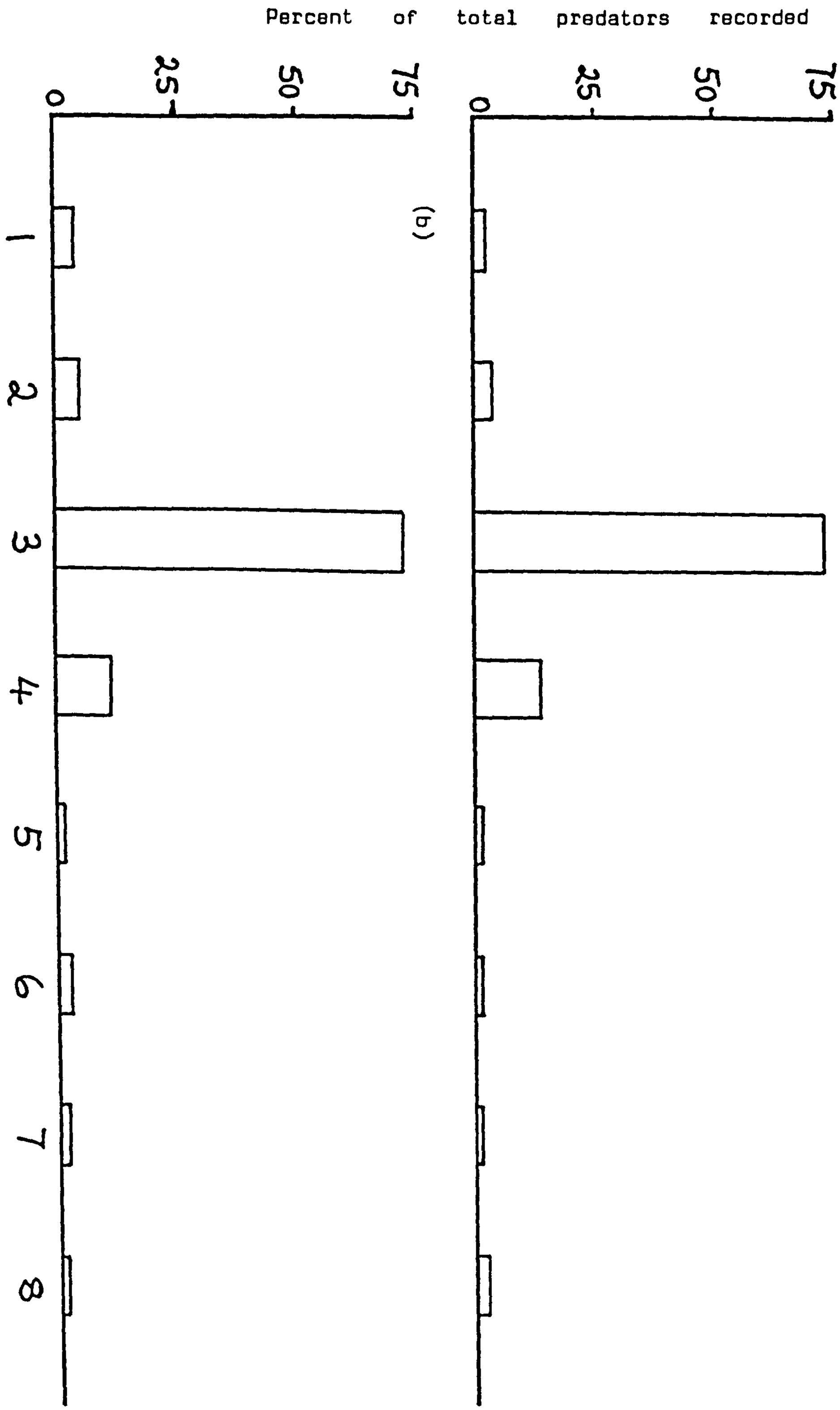

Percent of total predators recorded
0
25
50
75
(a)
(b)
1
2
3
4
5
6
7
8

Figure 64:

Abundance of B.angulatus on LF 125 during 1984

(a) Section 1

(b) Section 2

Nymphs

Males

Females

Figure 65:

Parasitism in populations of P.alni on LF 125, 1984

(a) Section 1

(b) Section 2

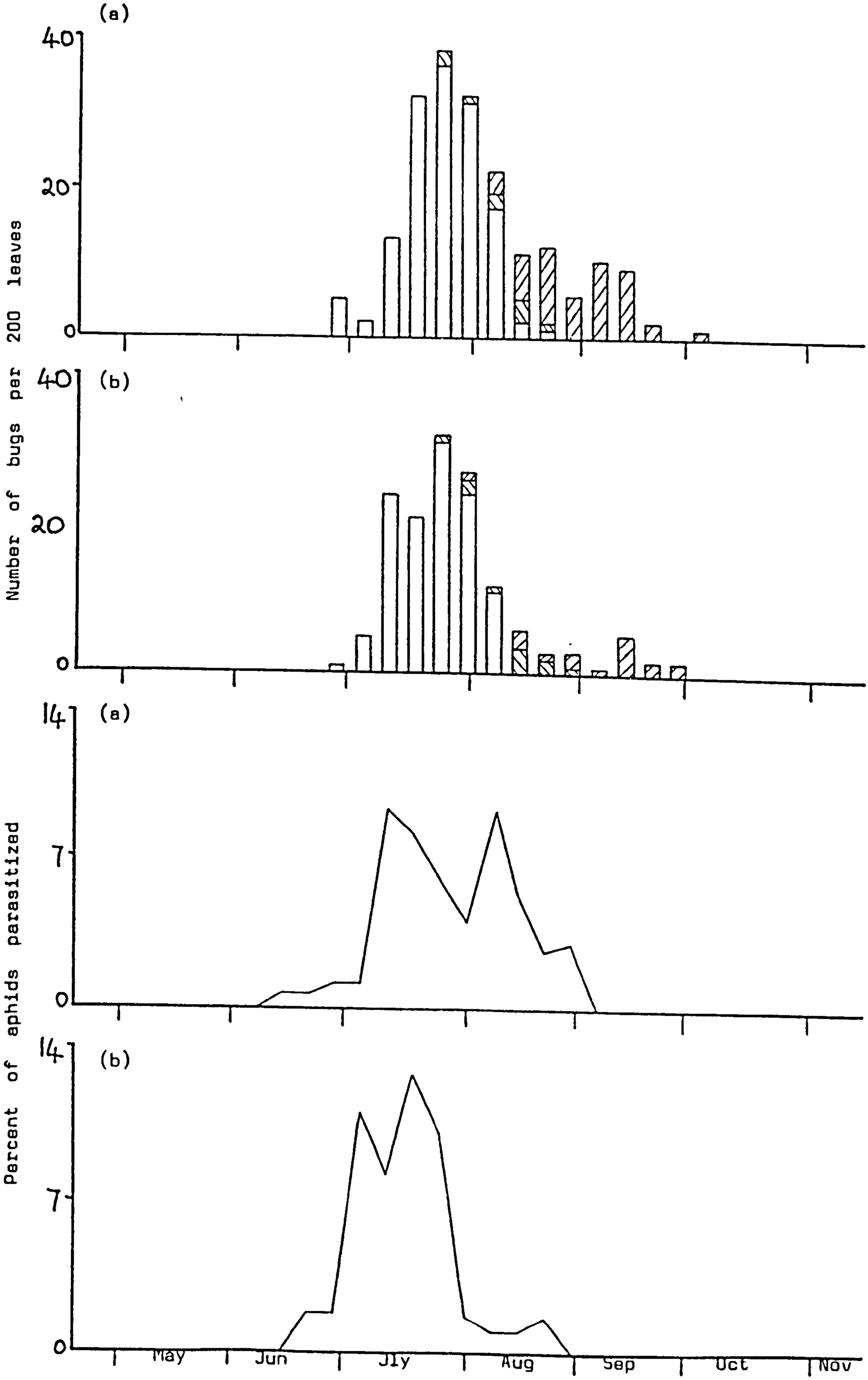
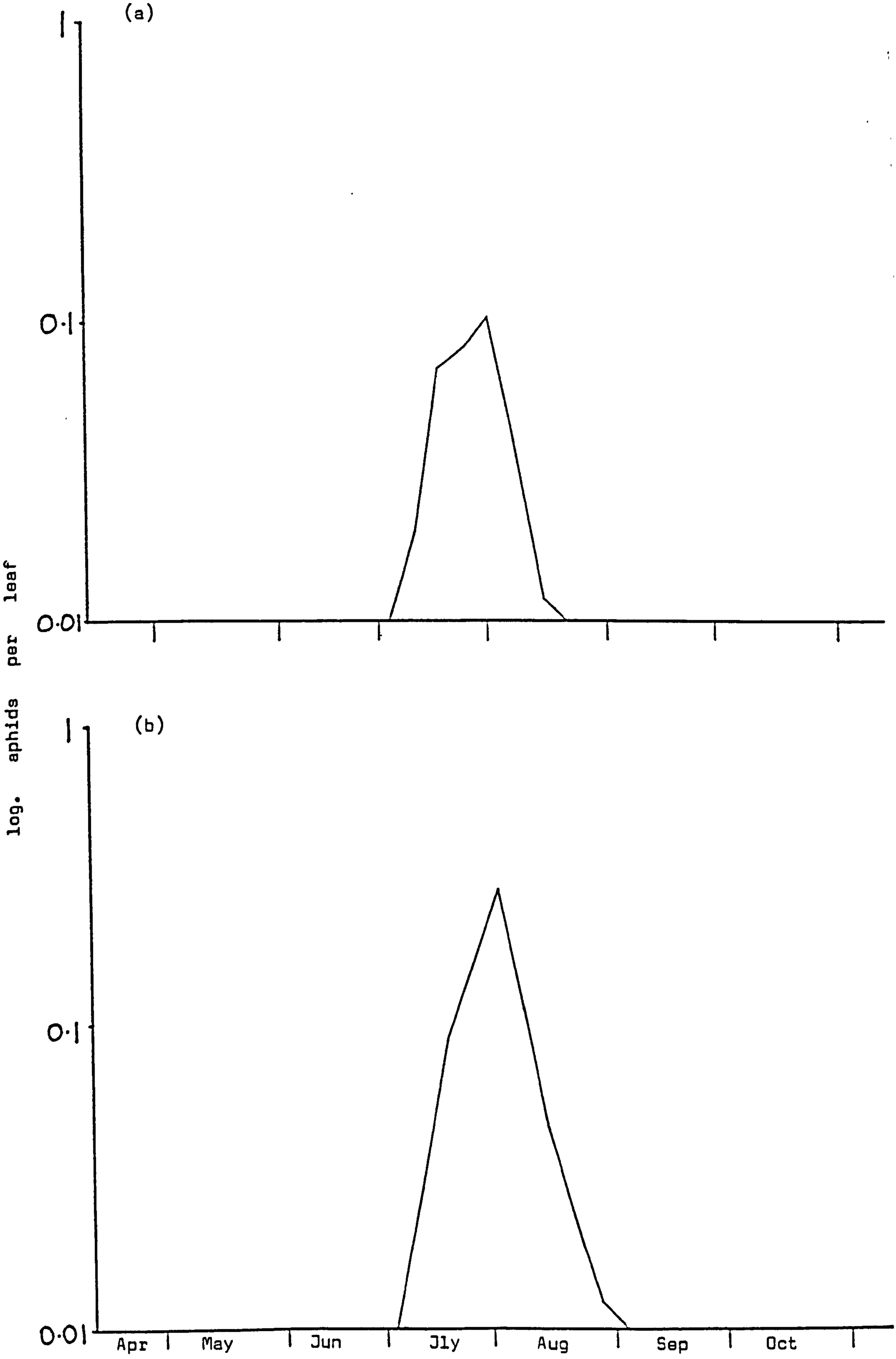

(a)
40
20
0
200 leaves
(b)
40
20
0
Number of bugs per
(a)
14
7
0
aphids parasitized
(b)
14
7
0
Percent of
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 66:

Aphid abundance on LF 126, 1984

(a) A.incana

(b) A.cordata


(a)
1
0·1
0·01
per leaf
(b)
log. aphids
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct

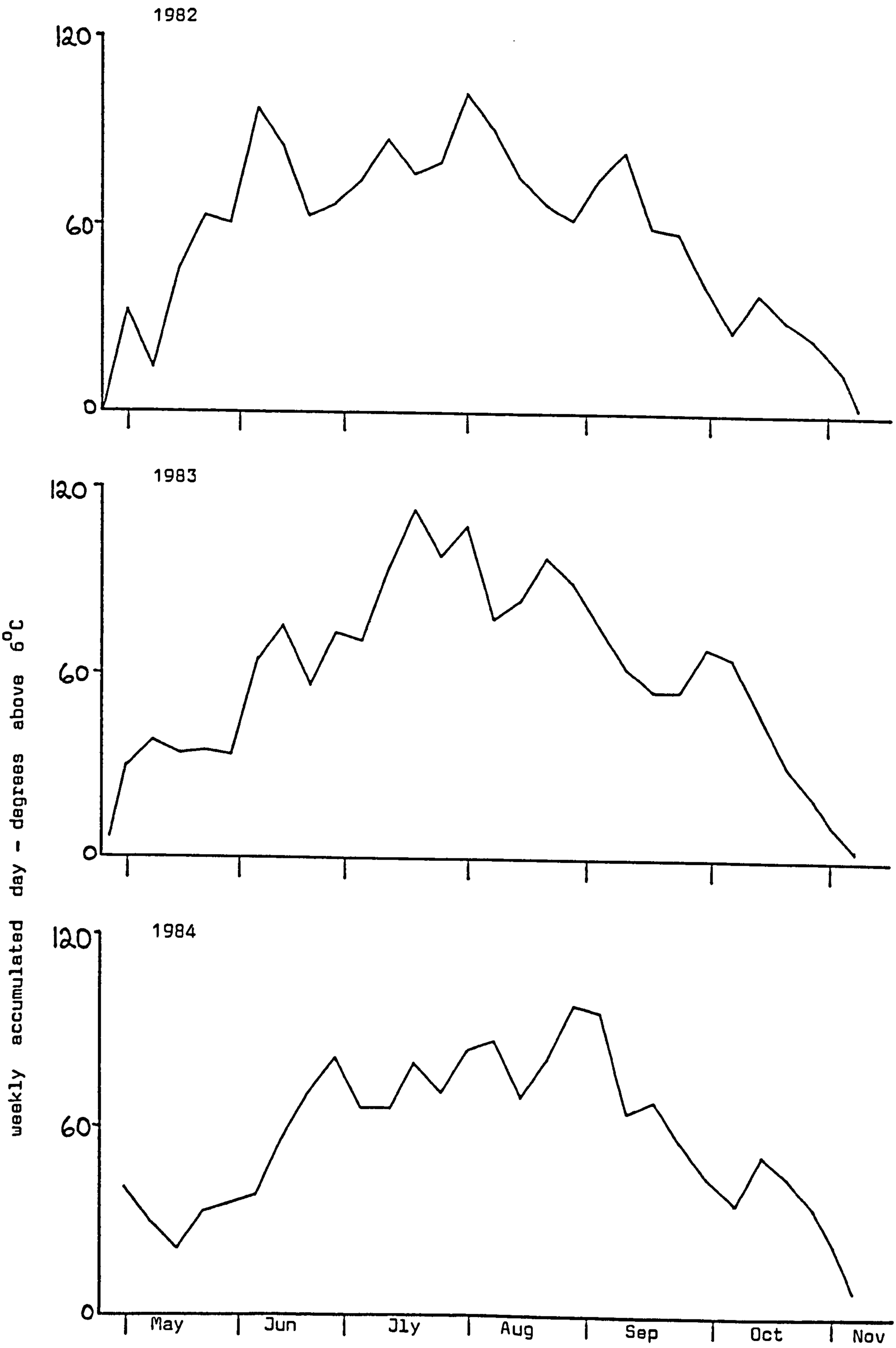


Figure 67: Temperature at East Malling

2.5.4. The between year dynamics of P.alni on LF125

Due to the effect of spraying there is little information to be gained from the populations which existed in 1982. Aphid numbers were low throughout the summer and predators present in the spring disappeared, either due to the spray or by emigration because of the disappearance of their prey. A notable exception to this was B.angulatus, nymphs of which hatched a month after spraying. More nymphs were found than adults ($d=2.17$, $p<0.05$). This difference may be due to greater activity of adults, and so less being found in leaf samples. It is also likely that emigration from the windbreak occurred, adults appearing on the mixed windbreak LF126, which was opposite LF125, at a similar time to their disappearance from LF125. Adults of S.ribesii oviposit on aphid infested plants (Alford, 1984) and E.balteatus young adults have been shown not to oviposit if aphids are absent (Chandler,1966, Schneider,1969), the response waning as the flies age. Neither of these species were found in 1982 when aphid numbers were low during the summer.

Alate aphids remained upon the windbreak although some emigration occurred early in the season, shown by arrivals on LF126 and aphids present on sticky traps (chapter 3). Although numbers appeared to be further reduced by pruning these gave rise to generations of apterous adults in late summer. With the increase in the soluble nitrogen level (chapter 5) and the fact that apterous adults are more fecund than alate ones (Dixon,1973) reproduction increased during September and relatively high numbers of oviparae were produced. There were more oviparae present in late October than there were aphids throughout the period after spraying and the peak numbers of oviparae on the leaves were similar to those of the fundatrices in the previous spring ($d=1.17$, $p>0.05$).

There were higher numbers of fundatrices present in spring 1983 than in 1982 ($d=5.09$, $p<0.001$). This was a likely result of the numbers of

oviparae present in autumn 1982. Due to the high numbers, the population increased rapidly with a rapid increase in the numbers of instars I-III during late May. The subsequent sharp decline in the population was also largely a result of a decline in the abundance of these nymphs. During the period of decline the nymphal proportion of the population fell from 60% to 50%, the rest of the population being alate adults. At the time of the population peak there was emigration of alates from the windbreak, shown by sticky trap data (chapter 3) and the arrival of alates on LF126. Thus the population decline on this windbreak appears to have been caused by similar factors to those previously described at Lyne. Nymphal production by apterous adults slowed down and the maturation of nymphs into alate adults followed by emigration caused the population to decline sharply.

During August and September numbers fell to very low levels, similar to those at the same times in 1982. However in 1983 predators were considerably more abundant than in 1982. In early August 1982, the predator/aphid ratio reached a peak of 1:1 whereas in 1983 it was 3:1 on the unpruned section and 6:1 on the pruned section. These predators were entirely adults of B.angulatus and were mostly female. The food consumption of B.angulatus was studied by Collyer (1952) who stated that adult females consumed over 2,900 adult specimens of P.ulmi, the fruit tree red spider mite during their adult life and males over 2,500. Alford (1984) states that the figure for females is 'over 3,000'. Glen (1973) expressed consumption in terms of dry weight of lime aphids eaten and stated that adult males ate 0.216mg of aphids per day and females between 0.334mg and 0.520mg. It may thus be seen that B.angulatus is a voracious predator. If the assumption is made that the bug consumes a similar weight of P.alni per day as it does E.tiliae this would represent a consumption of 3-4 adults or about 60 1st instar nymphs daily. It is therefore likely that the abundance of predators

restricted recovery of aphid numbers in 1983 whereas this had not been the case in 1982.

In spring 1984 there were fewer fundatrices present than in 1983 ($d=5.65$, $p < 0.001$) (table 33) and the population build up was less rapid due to the lower numbers present. Temperatures were similar during the two springs and thus the different increases in numbers appeared to be largely as a result of the differing initial numbers of fundatrices. The 1984 populations began increasing rapidly when the second generation adults began reproduction in mid June (table 14). The sharp decline in numbers was again due to the decline in nymphs born and those already present maturing and becoming alate.

Predator/aphid ratios were high on both sections as in 1983. On the unpruned part the ratio reached 10:1 in mid September and on the pruned section 1.5:1. These values were again caused by the presence of B.angulatus females on the windbreak. The extreme value on the unpruned section was due to the bugs being present in higher numbers and there being fewer aphids. It is therefore likely that aphid numbers in late summer were kept at a low level by the action of the predators. Only when the adult bugs disappeared did the aphid populations recover slightly due to the reproduction of fifth and sixth generation adults in early October.

It is unlikely that predators played a major role in limiting population build-up. The main predator present early in the year was O.marginalis. This partially predacious bug (Southwood and Leston,1959, Alford 1984) occurred in small numbers and it is therefore unlikely that it limited aphid population increase. It was noticeable that this bug disappeared rapidly when the windbreak was sprayed in 1982 and this finding is in keeping with Alford (1984) who states that it is most numerous in unsprayed

Table 14 RELATIVE POPULATION GROWTH RATES PER DAY $\left[LnN_2-LnN_1\ (t_2-t_1)^{-1}\right]$ LF125,1983 and 1984

1983		1984		
Date	Section(1+2)	Date	Section 1	Section 2
25/4- 2/5		30/4- 7/5	0.220	0.240
2/5- 9/5	0.08	7/5-14/5	0.180	0.140
9/5-16/5	0.02	14/5-21/5	0.090	0.007
16/5-23/5	-0.01	21/5-28/5	0.004	0.210
23/5-30/5	0.22	28/5- 4/6	0.130	0.008
30/5- 6/6	0.07	4/6-11/6	-0.120	-0.030
6/6-13/6	0,05	11/6-18/6	0.200	0.100
13/6-20/6	0.06	18/6-25/6	0.040	0.090
20/6-27/6	0.05	25/6- 2/7	0.003	0.005
27/6- 4/7	0.06	2/7- 9/7	0.060	0.030
4/7-11/7	0.03	9/7-16/7	0.160	0.230
Over total period	0.06		0.09	0.09

orchards.

In 1983 and 1984 the windbreak was pruned whilst the aphid population was declining. Aphid numbers fell by a similar amount on both the unpruned and pruned sections in both years. Pruning occurred at the time of bug migration and did not appear to affect the number on the windbreak.

Aphid populations on this windbreak thus showed similar patterns of abundance to those described previously at Lyne. Aphids were considerably more abundant at East Malling, population peaks in terms of aphids per leaf being 20-30 times greater on the windbreak compared to the branches at Lyne. However similar factors appeared to determine numbers. Temperature played less of a part in early season build up, due to the high numbers present compared to Lyne. Predators were more abundant at East Malling and are likely to have exerted a greater influence on aphid numbers following the major decline period.

Aphid populations did not exist for long on A.cordata and A.incana and were initiated each summer by the arrival of alate individuals. Although these two alders can provide an acceptable food source for P.alni, shown by caging experiments (chapter 5) populations were not sustained for long. Predators were virtually absent so it is unlikely that their action may have affected aphid numbers. Other mortality factors, such as the weather and especially wind may play a part in reducing aphid numbers.

2.5.5. WM110, 1982

(i) Abundance of aphids

The windbreak WM110 (A.glutinosa) was divided into two sections at the beginning of the season. One section was left unpruned and the other cut between July 15th - 22nd. The uncut section was further subdivided in winter 1982/83 when half of it was cut and half left untouched. The

section left uncut for a year will hereafter be referred to as 'section 1', that left in summer but cut in winter as 'section 2', and that cut as normal in summer only as 'section 3'.

Aphids hatched in late April but initial numbers were low. The population began increasing rapidly during June, as the second generation adults became mature and started reproducing (figs.68a,69a). The population on section (1+2) reached its peak on July 29th and subsequently declined sharply to low levels during September, with a small resurgence in October. Section 3 was pruned between July 15th and 22nd. If section (1+2) is taken as the control this was two weeks before the population would have peaked. Numbers previous to July 15th were similar on both sections and so this assumption appears justified. Pruning had a marked effect on aphid numbers, reducing them considerably. The population reached very low levels in September but recovered during the autumn (table 15).

The pattern of abundance on terminal and non terminal leaves was similar on both sections and mirrored that of the total population (figs.68b,69b). Pruning caused a reduction in the numbers on both sorts of leaf but the decline was steepest on the terminals.

As happenedon LF125, the density of aphids was greatest on terminal leaves throughout most of the period of population build-up (fig.70 a,b). The trend was reversed on section (1+2) after leaf growth had ceased and the population declined. On section 3 it was reversed after pruning.

The age structure of the populations is shown in figs.71 and 72. Throughout the period of population growth instars I-III accounted for between 60-80% of the total population. After the population peaked on section (1+2) the figure remained above 60% for the rest of the season

Fig.68:

Aphid abundance on WM 110, section (1 + 2) 1982

(a) 200 leaf sample

(b) 100 leaf samples:

- - - Terminal leaves

——— Non-terminal leaves

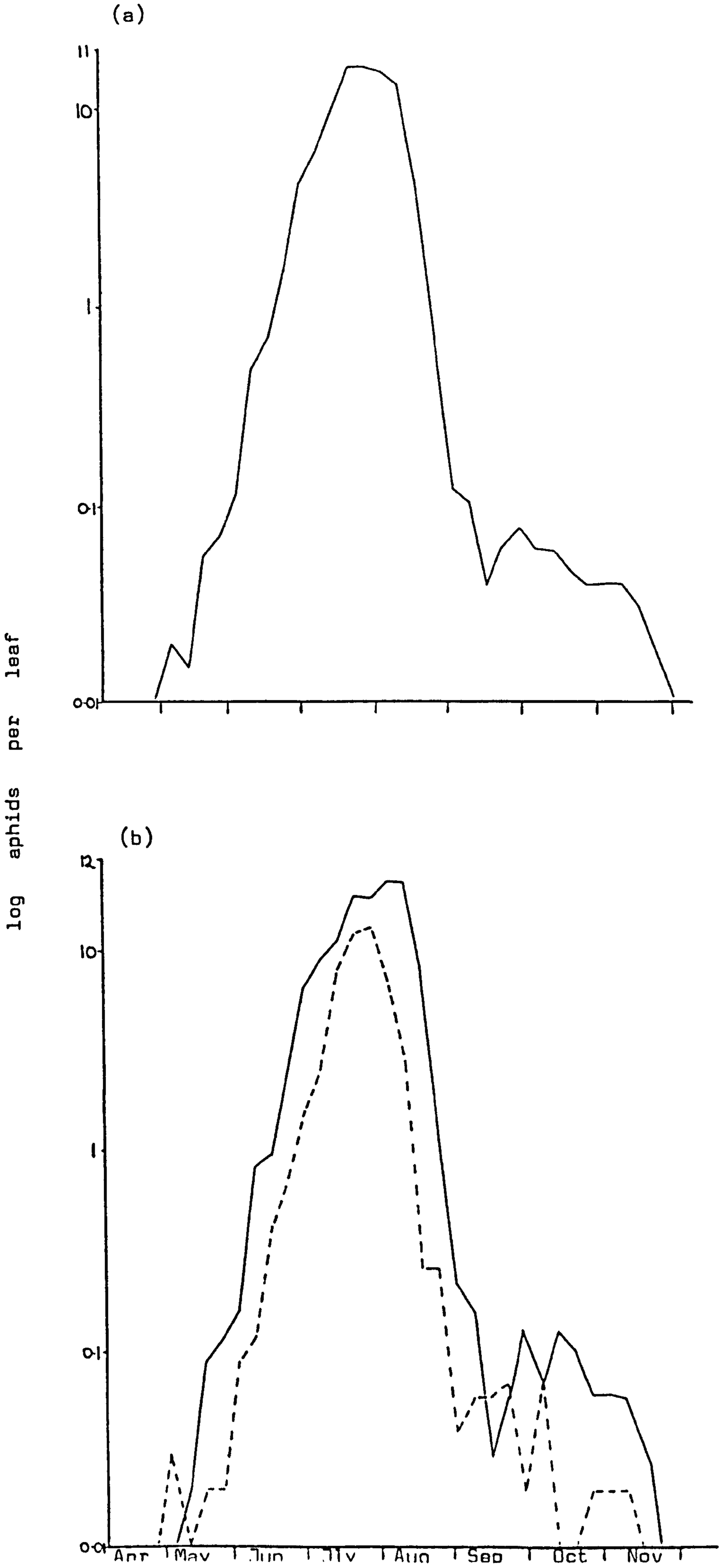

(a)
11
10
1
0·1
0·01
log aphids per leaf
(b)
2
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 69:

Aphid abundance on WM 110, section 3, 1982

(a) 200 leaf sample

(b) 100 leaf samples:

- - - Terminal leaves

——— Non-terminal leaves

Arrows represent date of pruning

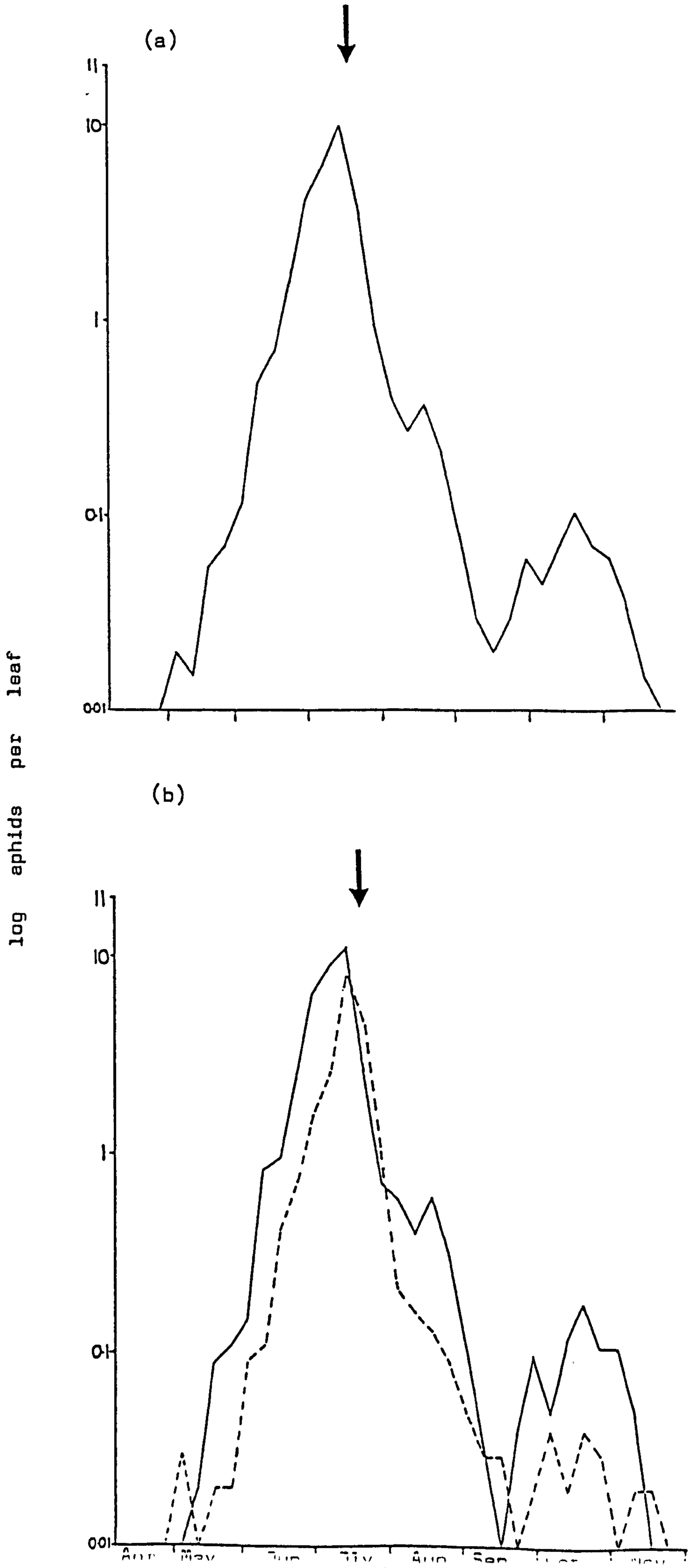

(a)
11
10
1
01
001
leaf
log aphids per
(b)
11
10
1
01
001
Aug
May
Jun
Jly
Aug
Sep

Table 15 TOTAL NUMBER OF APHIDS IN LEAF SAMPLES - WM110, 1982

		S E C T I O N (1+2)			S E C T I O N 3		
Date		Aphids/100 Terminal	Aphids/100 Non-terminal	Aphids/ Whole sample	Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample
April	29	0	0	0	0	0	0
May	6	2	0	2	2	0	2
	13	0	1	1	1	1	2
	20	1	8	9	2	9	11
	27	1	11	12	1	11	12
June	3	8	15	23	6	20	26
	10	11	85	96	14	84	98
	17	42	97	139	40	110	150
	24	73	242	315	77	253	330
July	1	160	681	841	143	727	870
	8	263	939	1202	224	989	1213
	15	823	1153	1976	791	1107	1898
	22	1248	1982	3230	492	268	760
	29	1345	1932	3277	110	72	182
Aug	5	732	2346	3078	20	60	80
	12	312	2325	2637	15	39	54
	19	26	851	877	12	62	74
	26	26	124	150	8	32	40
Sept	2	2	22	24	4	10	14
	9	4	15	19	2	2	4
	16	4	2	6	2	0	2
	23	5	5	10	0	4	4
	30	1	12	13	1	9	10
Oct	7	5	12	17	3	4	7
	14	0	12	12	1	11	12
	21	0	18	18	3	16	19
	28	1	15	16	2	10	12
Nov	4	1	12	13	0	10	10
	11	1	7	8	1	4	5
	18	0	4	4	1	0	1

Figure 70:

Population density of P.alni on WM 110 1982

(a) Section (1 + 2)

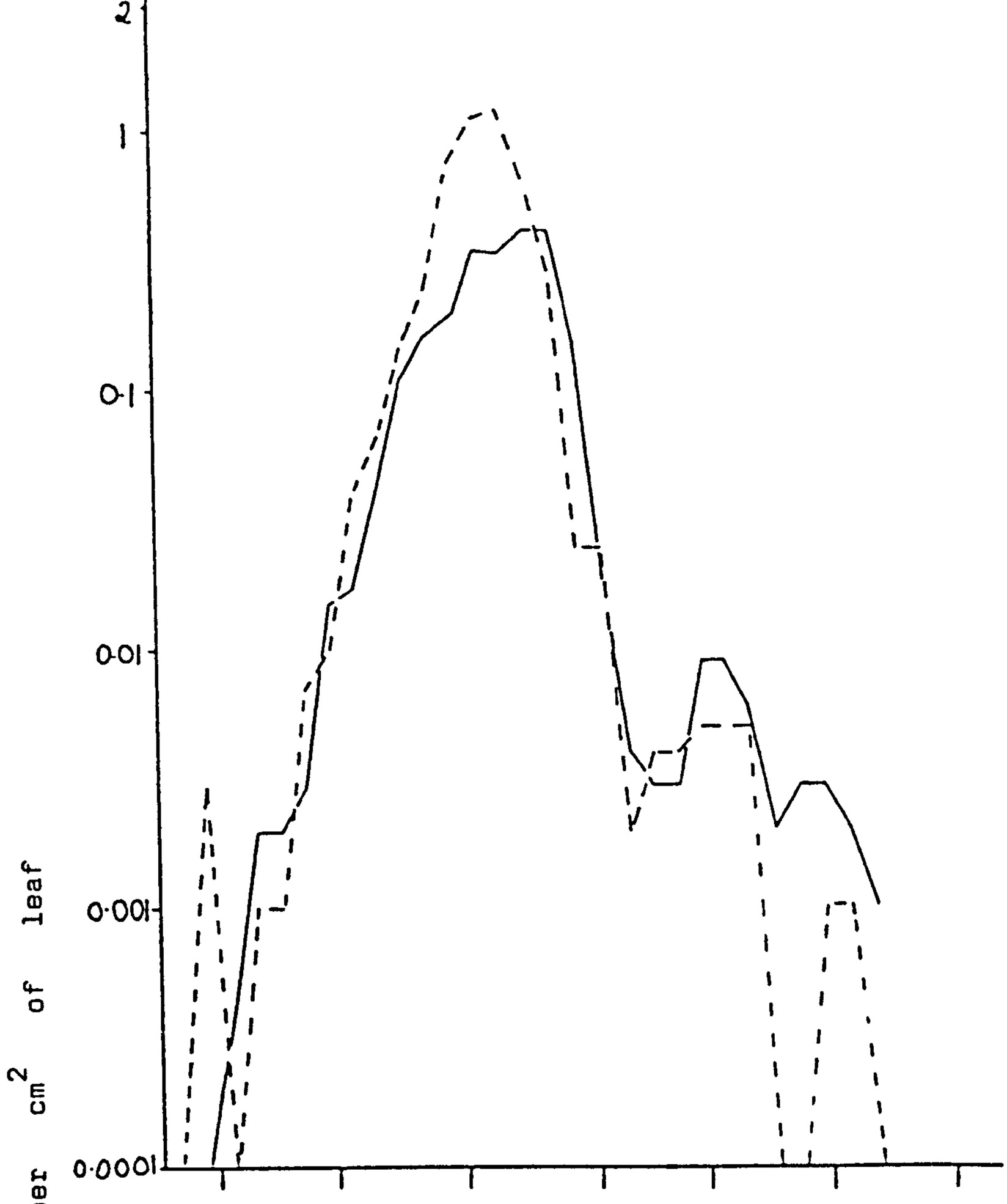
(b) Section 3

- - - - Terminal leaves

——— Non-terminal leaves

Arrow represents date of pruning

(a)


2
1
0·1
0·01
0·001
0·0001
log. aphids per cm² of leaf

(b)

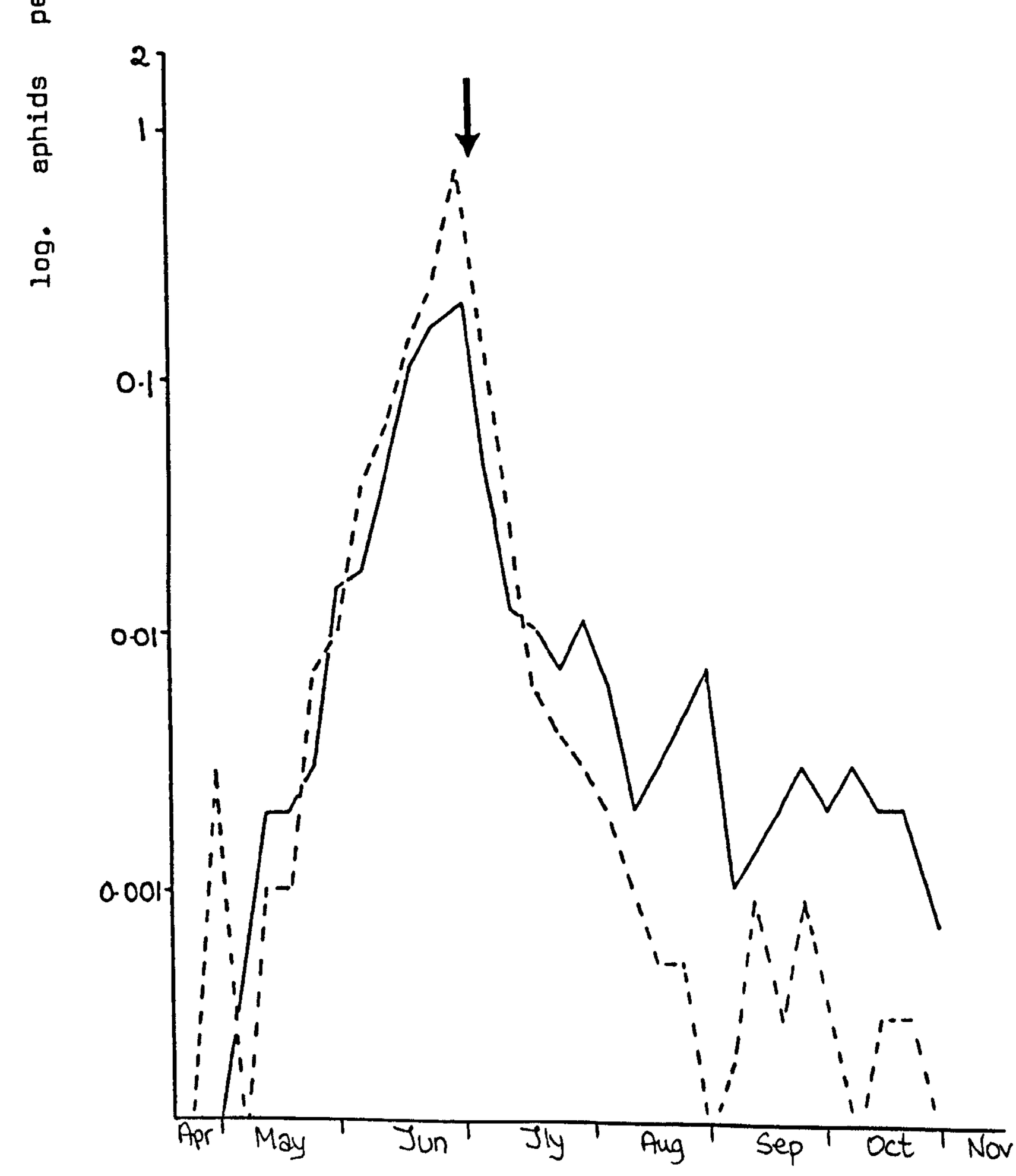

2
1
0·1
0·01
0·001
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 71:

Age structure of the population on WM 110

section (1 + 2), 1982

(i) Alate adults

(ii) Fourths (presumptive alatae)

(iii) Apterous adults

(iv) Fourths (presumptive apterae)

(v) Nymphs

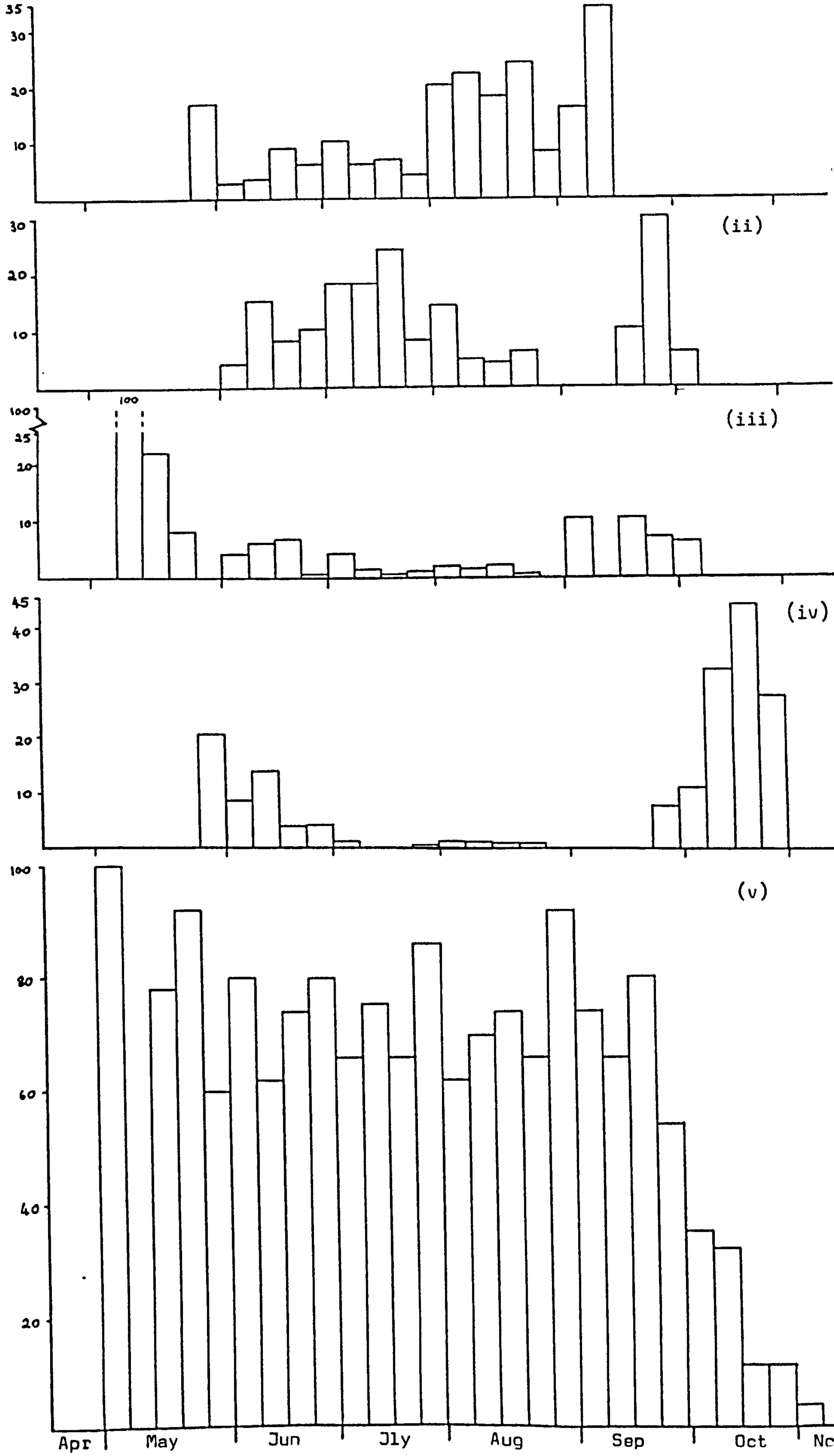
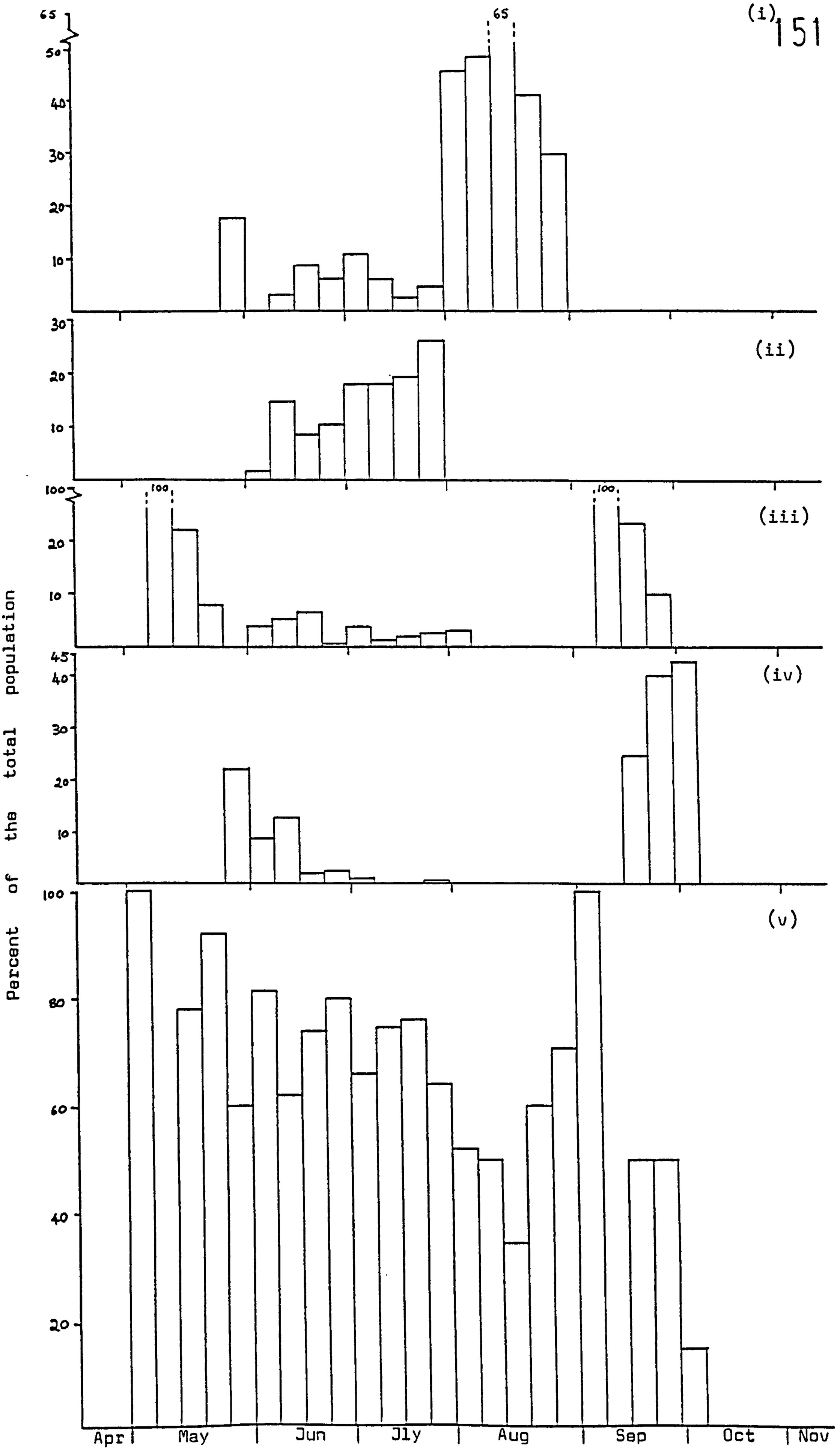

35
30
20
10
(ii)
30
20
10
100
25
20
10
(iii)
Percent of the total population
45
40
30
20
10
(iv)
100
80
60
40
20
(v)
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 72:

Age structure of the population on WM 110

section 3, 1982

Legend as for figure 71


(i)
65
65
50
40
30
20
10
(ii)
30
20
10
(iii)
100
100
100
20
10
(iv)
45
40
30
20
10
(v)
100
80
60
40
20
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

until October when sexual forms began to form a large part of the population. After pruning on section 3 the proportion of nymphs fluctuated widely. Alate adults comprised 65% of the population during mid August and apterous adults reached high proportions during September. Alate adults were recorded before any alate fourth instars were found. It is likely that these arrived from other alder similar to the occurrence at Lyne in 1983. The fundatrices gave rise to a second generation which was mostly apterous and the third and fourth generations were mostly alate. The fifth generation was mostly apterous and the sixth entirely so. The seventh and last generation were the sexual forms.

There were differences in the age structure of the populations on terminal and non terminal leaves (appendix 2.5). There was a greater proportion of fourth instars (presumptive alatae) on terminal leaves and a greater proportion of alate adults on non terminals during the period of population build-up. Alate forms first appeared in early July and at the time of the population peak the fourth instar was entirely alate (fig 73a,b). Alate adults continued to be produced until late August on section (1+2) but none were found after August 5th on section 3. Sexual forms appeared from early October (fig 74a,c). Oviparae persisted until late November and final numbers were higher on section 3 (fig74b,d).

(ii) Spatial distribution of aphids

On section (1+2) the value for b in Taylor's power law was 1.47 for terminal leaves and 1.43 for non terminals.On section 3 these values were 1.48 and 1.38 respectively (table 26). These values are significantly different from unity indicating that the aphids were aggregated over the whole season. The values of Morisita's index showed a similar pattern to those described for LF125 in 1983 and 1984 (table 16). High to begin with it fell during the period of population increase, rising again in

Figure 73:

Proportion of presumptive alatae in the

fourth instar, WM 110 1982

(a) Section (1 + 2)

(b) Section 3

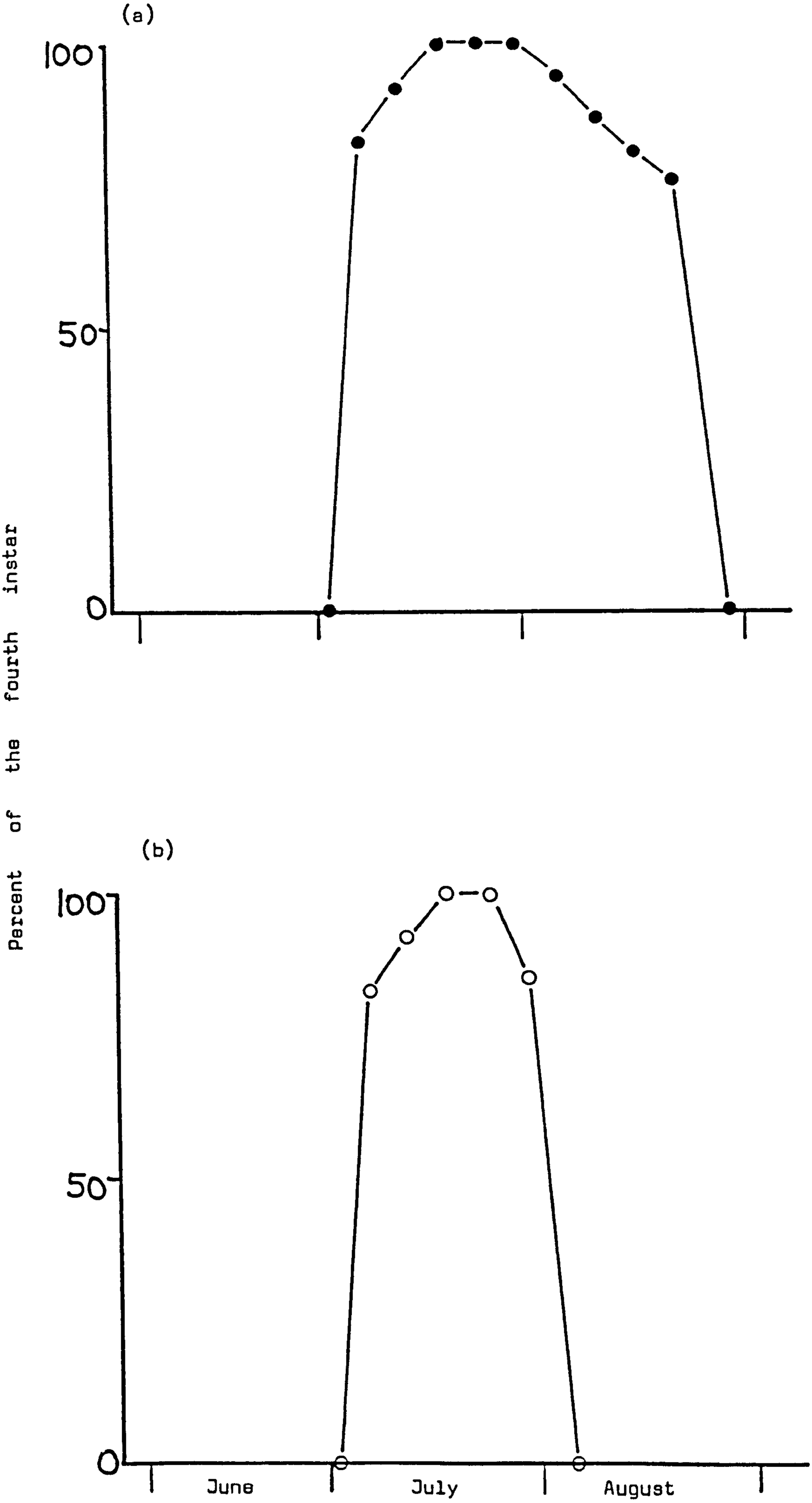

(a)
100
50
0
Percent of the fourth instar
(b)
100
50
0
June
July
August

Figure 74:

Abundance of sexuales, WM110 1982

(a) Appearance of sexuales, section (1 + 2)

(b) Abundance of oviparae, section (1 + 2)

(c) Appearance of sexuales, section 3

(d) Abundance of oviparae, section 3

Males

Oviparae

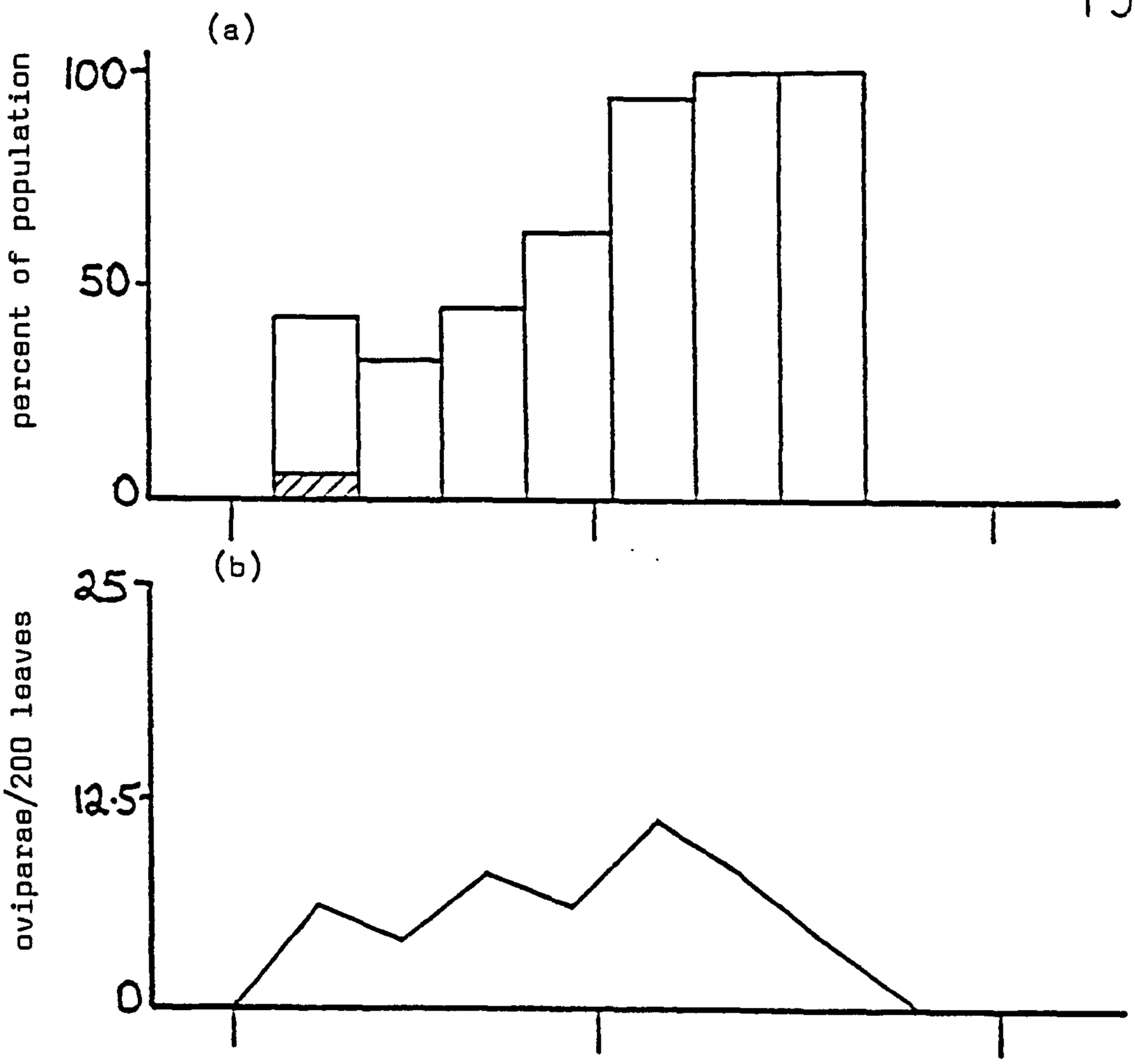

(a)
100
50
0
percent of population
(b)
25
12.5
0
oviparae/200 leaves
(c)
100
50
0
percent of population
(d)
25
12.5
0
oviparae/200 leaves
October
November

Table 16 MORISITA'S INDEX OF DISPERSION - WM110, 1982

Date		S E C T I O N (1+2)		S E C T I O N 3	
		Terminal leaves	Non-terminal leaves	Terminal leaves	Non-terminal leaves
April	29				
May	6	0		0	
	13		0	0	0
	20	0	75.0	0	31.6
	27	0	81.8	0	74.3
June	3	27.3	11.4	17.3	15.3
	10	5.5	4.5	8.3	3.6
	17	2.4	3.1	7.6	3.2
	24	4.8	2.9	4.3	2.4
July	1	4.4	3.1	4.0	2.6
	8	5.1	3.8	5.3	2.4
	15	5.7	2.5	5.7	2.7
	22	2.7	2.8	5.1	2.8
	29	3.1	2.3	12.5	3.4
Aug	5	4.7	1.5	12.1	4.6
	12	4.7	2.3	2.4	3.8
	19	6.4	2.3	13.3	1.7
	26	1.9	2.0	0	7.9
Sept	2	0	3.6	0	5.0
	9	0	0	0	0
	16	0	4.2	0	
	23	0	0		0
	30	0	10.3	0	0
Oct	7	8.7	1.8	28.6	0
	14		10.6	0	1.8
	21			0	16.7
	28	0		0	0
Nov	4	0			0
	11	0	0	0	0
	18			0	

late summer as the population became patchy and finally falling to zero as aphids became evenly distributed, singly on the leaves occupied.

(iii) Abundance of natural enemies

The total number of predators found each week is shown in fig.75a,c. The numbers were similar on both sections of the windbreak ($d=0.85, d.f.=33, p>0.05$) over the season. Pruning did not appear to affect predator abundance as it did the aphids. At the time of pruning in mid July, the only predators were nymphs and adults of B.angulatus. The egg hatching period of B.angulatus can continue until early August (Alford,1984) and numbers increased until the end of July on the unpruned section. Winged adults may return to the tree if dislodged by the cutter. These two factors may combine to keep predator numbers steady following pruning.

The ratio of predators to aphids followed a similar trend on both sections (fig.75b,d). Early season appearances by A.bipunctata and A.nemorum adults caused the ratio to be high during May. During the period of build-up in aphid numbers the ratio remained low at around 1 predator per 1000 aphids found. When the aphid number decreased following pruning on section 3 the ratio rose rapidly to reach a maximum value of 1 predator to every 2 aphids in mid September. Aphid numbers did not decrease as early on the unpruned section and consequently the ratio did not begin to rise until later in the season, reaching a maximum value of 1 per 6 aphids found. A.bipunctata was the only coccinellid and A.nemorum the only anthocorid found during the season. Small numbers of C.carnea, P.ambiguus and O.marginalis were recorded. One syrphid larva was found on section (1+2) and was of E.balteatus. A solitary larva of Aphidoletes aphidimyza was found on section 3. B.angulatus was the commonest predator, accounting for 75% of total numbers found on each section (fig.76a,b,). Nymphs first appeared in late June and adults from late July onwards. Adult females persisted until late September (fig.77a,b).

Figure 75:

Abundance of predators, WM 110, 1982

(a) Total number of predators, section (1 + 2)

(b) Ratio of predators to aphids, section (1 + 2)

(c) Total number of predators, section 3

(d) Ratio of predators to aphids, section 3

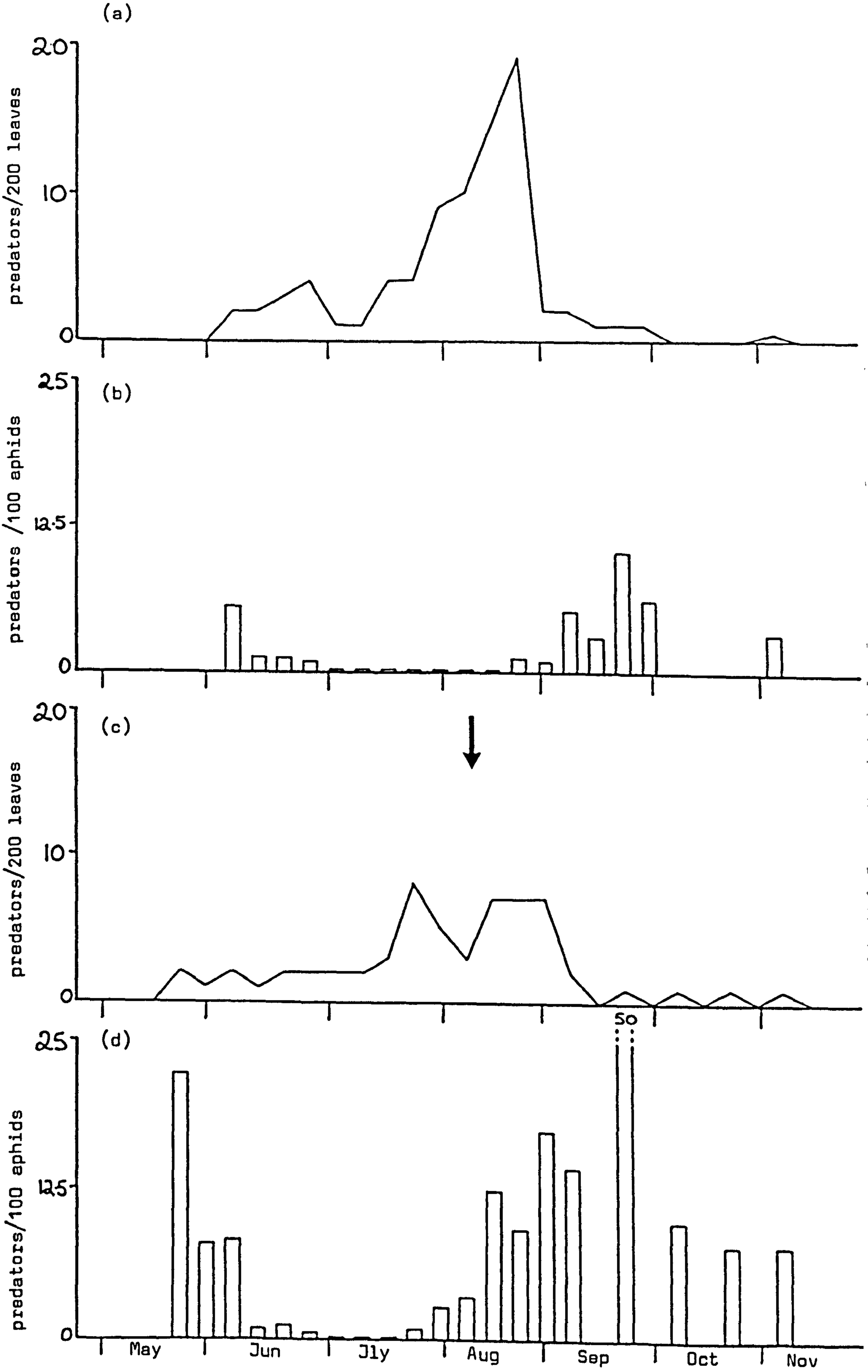

(a)
20
10
0
predators/200 leaves
(b)
25
12.5
0
predators /100 aphids
(c)
20
10
0
predators/200 leaves
50
(d)
25
12.5
0
predators/100 aphids
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 76:

Relative abundance of predators by groups,

WM 110, 1982

(a) section (1 + 2)

(b) section 3

(1) Coccinellidae

(2) Anthocoridae

(3) B.angulatus

(4) O.marginalis

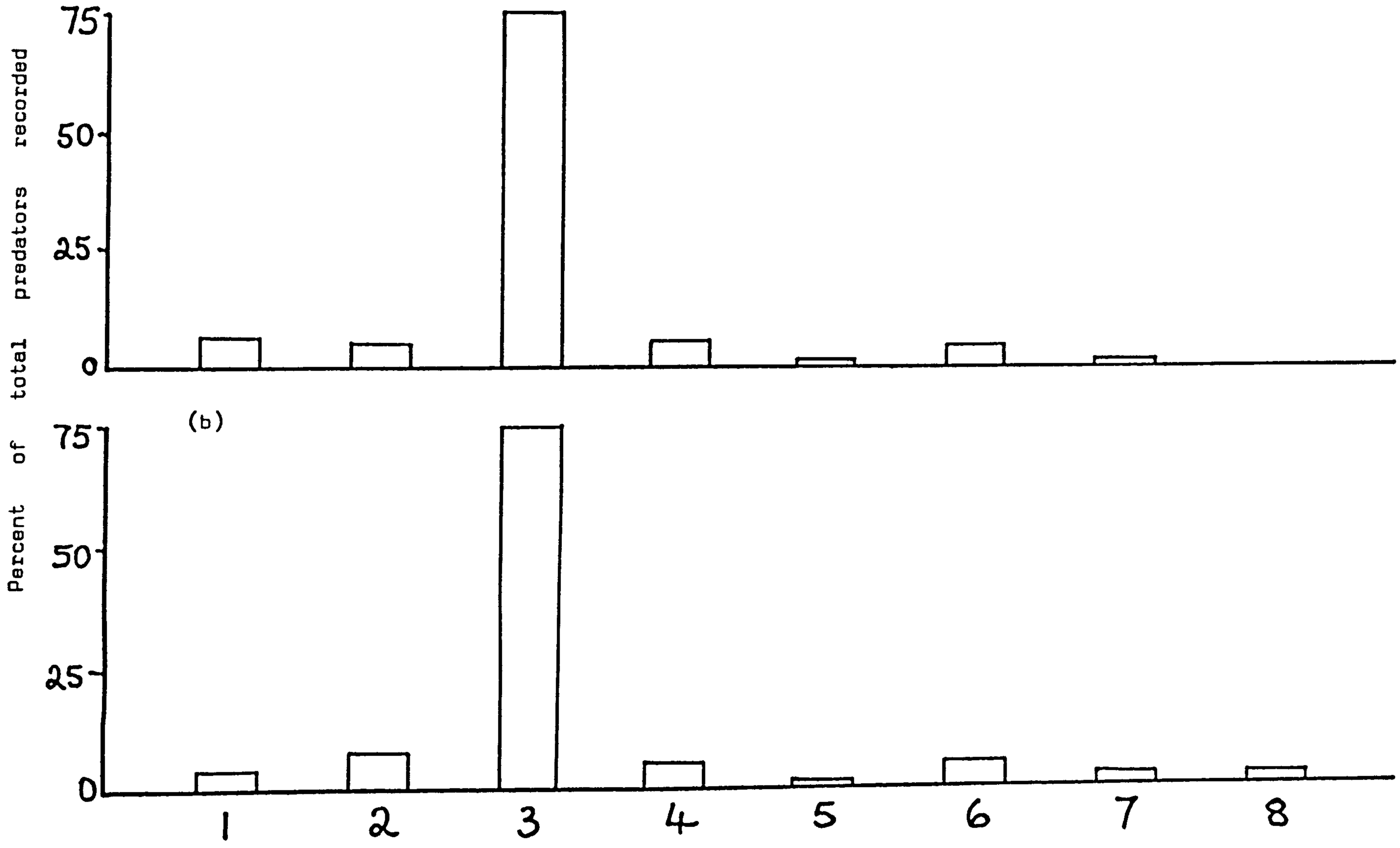
(5) P.ambiguus

(6) Neuroptera

(7) Syrphidae

(8) Cecidomyiidae

(a)



(b)

Figure 77:

Numbers of B.angulatus on WM 110, 1982

(a) Section (1 + 2)

(b) Section 3

Nymphs

Males

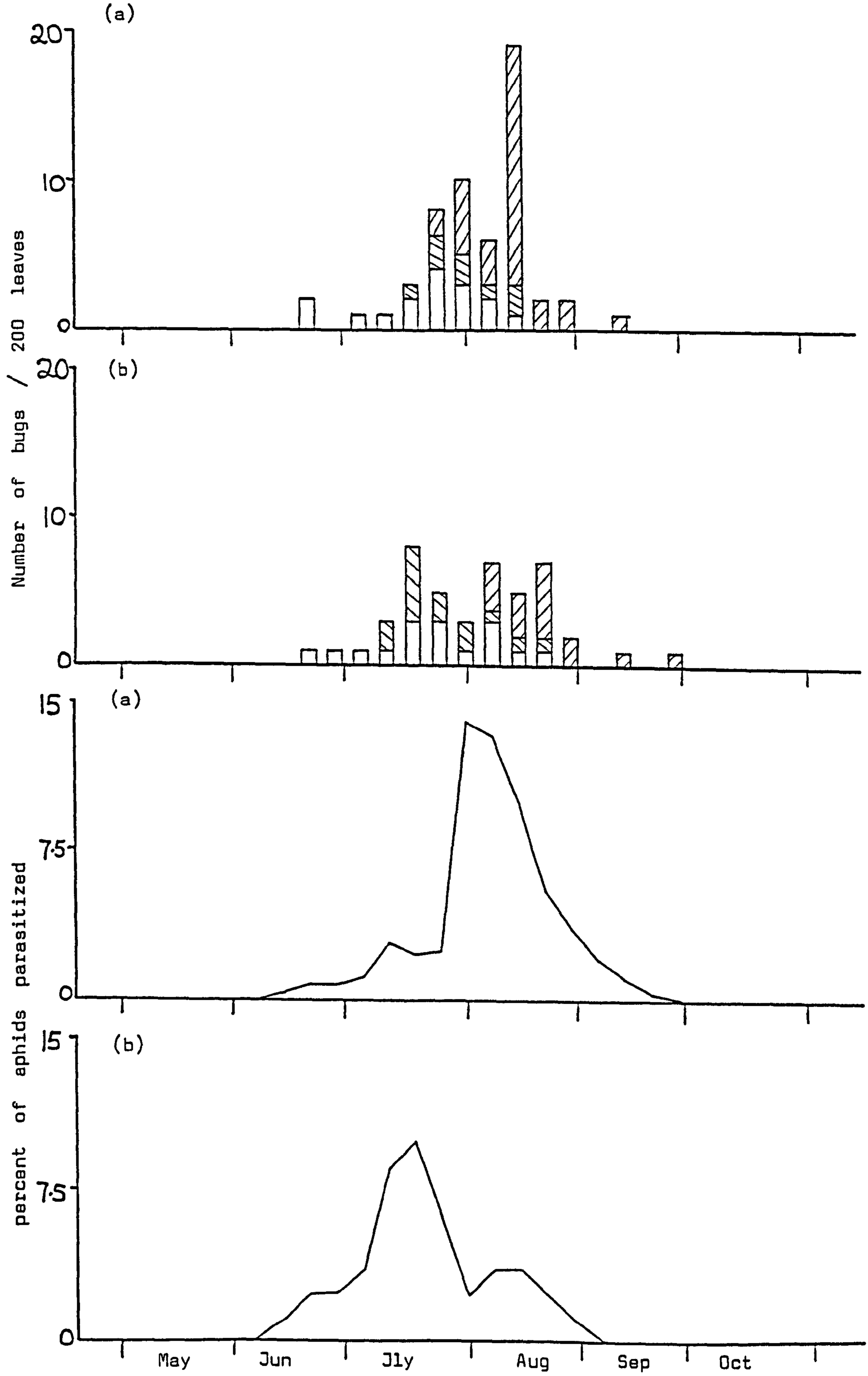
Females

Figure 78:

Parasitism in populations of P.alni on WM 110, 1982

(a) Section (1 + 2)

(b) Section 3


(a)
20
10
0
200 leaves
(b)
20
10
0
Number of bugs /
(a)
15
7·5
0
(b)
15
7·5
0
percent of aphids parasitized
May
Jun
Jly
Aug
Sep
Oct

Parasitism by T.pallidus was first observed in mid June. On section 3 this reached a peak of 9.9% in late July and 14.1% on section (1+2) in early August (fig.78 a,b), there being no significant difference between these figures (d = 0.676, p 0.05). No examples of Praon cocoons were found nor any aphids killed by Entomophthora spp.

2.5.6. WM109, 1982

(i) Abundance of aphids

WM109 was a pure A.cordata windbreak and existed in two sections to the north and south of WM110 (fig 1b). The section to the south was pruned between July 22nd and 29th and that to the north left uncut during the summer and pruned the following winter. No aphids were found on the uncut section throughout April and May. In early June alatae and first instar nymphs were recorded and the population began to gradually increase (figs.79 and 80). Numbers remained at relatively low levels compared to those on WM110 and appeared to be reinforced by alate adults arriving and beginning to reproduce (table 17). Numbers on terminal and non-terminal leaves followed a similar pattern although fewer aphids were found on the terminals (figs.79 and 80). Numbers increased on the cut section soon after pruning (fig.80) and this appeared to be due to an influx of alates which began reproducing (table 17). The age structure of the populations on each section indicated that instars I-III generally accounted for 60-100% of the total numbers (figs.81 and 82). For parts of the season the population consisted of only alate adults and these young nymphs. The nymphs from the first alate arrivals appeared to produce a generation of apterous adults. The following generation contained mostly alatae and in mid August the fourth instar was entirely presumptive alatae. The next generation was apterous and offspring from these were the sexual generation which appeared during October. These generations were most noticeable on the cut section (fig.82), possibly due to the higher numbers of aphids

Figure 79:

Aphid populations on WM 109, A.cordata,

Section A, 1982

(a) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

(b) 200 leaf sample

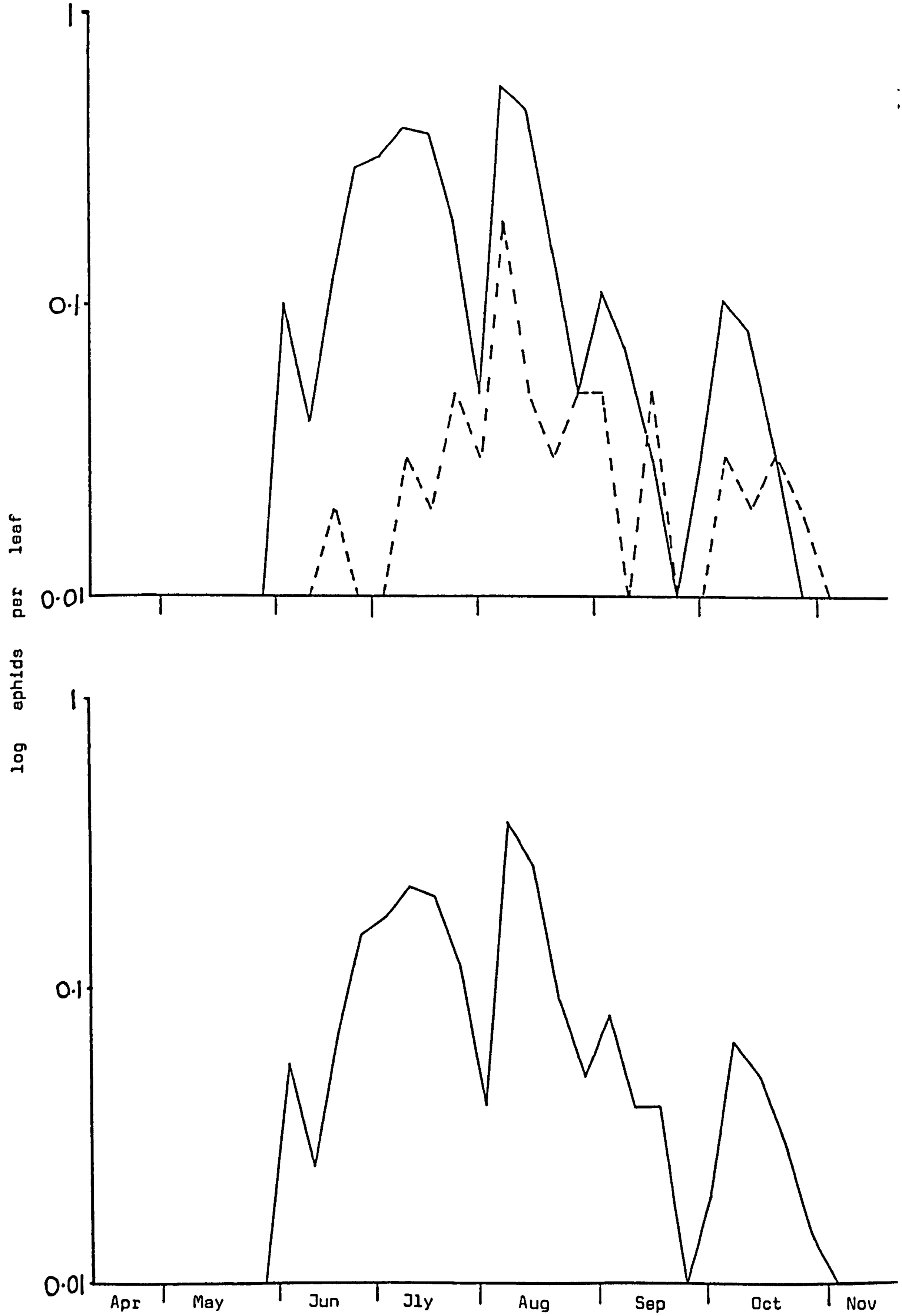

log aphids per leaf
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 80:

Aphid populations on WM 109, A.cordata,

Section 8, 1982

(a) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

(b) 200 leaf sample

Arrow represents date of pruning

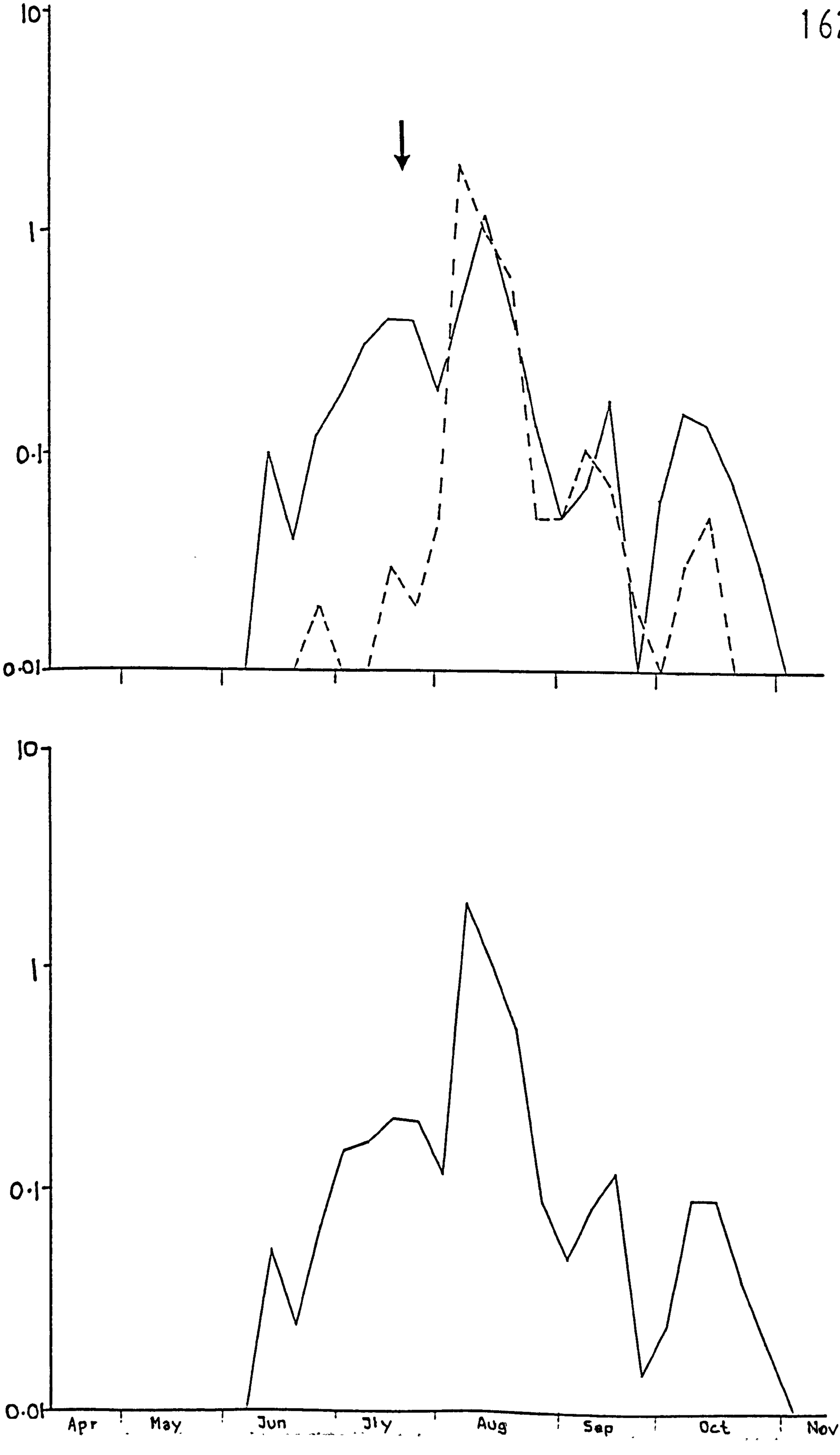

log aphids per leaf
10
1
0·1
0·01
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Table 17 TOTAL NUMBERS OF APHIDS IN LEAF SAMPLES - WM109,1982

Date		S E C T I O N A			S E C T I O N B		
		Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample	Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample
April	29	0	0	0	0	0	0
May	6	0	0	0	0	0	0
	13	0	0	0	0	0	0
	20	0	0	0	0	0	0
	27	0	0	0	0	0	0
June	3	0	9	9	0	8	8
	10	0	3	3	0	4	4
	17	1	11	12	1	9	10
	24	0	28	28	1	19	20
July	1	0	31	31	0	34	34
	8	2	40	42	2	44	46
	15	1	38	39	1	36	37
	22	4	18	22	3	21	24
	29	2	4	6	188	197	385
Aug	5	18	55	73	98	116	214
	12	4	46	50	62	46	108
	19	2	14	16	4	12	16
	26	4	4	8	4	4	8
Sept	2	4	10	14	9	6	15
	9	0	6	6	6	16	22
	16	4	2	6	1	0	1
	23	0	0	0	0	5	5
	30	0	2	2	2	14	16
Oct	7	2	9	11	4	12	16
	14	1	7	8	0	6	6
	21	2	2	4	0	2	2
	28	1	0	1	0	0	0
Nov	4	0	0	0	0	0	0
	11	0	0	0	1	0	1
	18	0	0	0	0	0	0

Figure 81:

Age structure of the population on WM 109 section A, 1982

(i) Alate adults

(ii) Fourth instars (presumptive alatae)

(iii) Apterous adults

(iv) Fourth instars (presumptive apterae)

(v) Nymphs

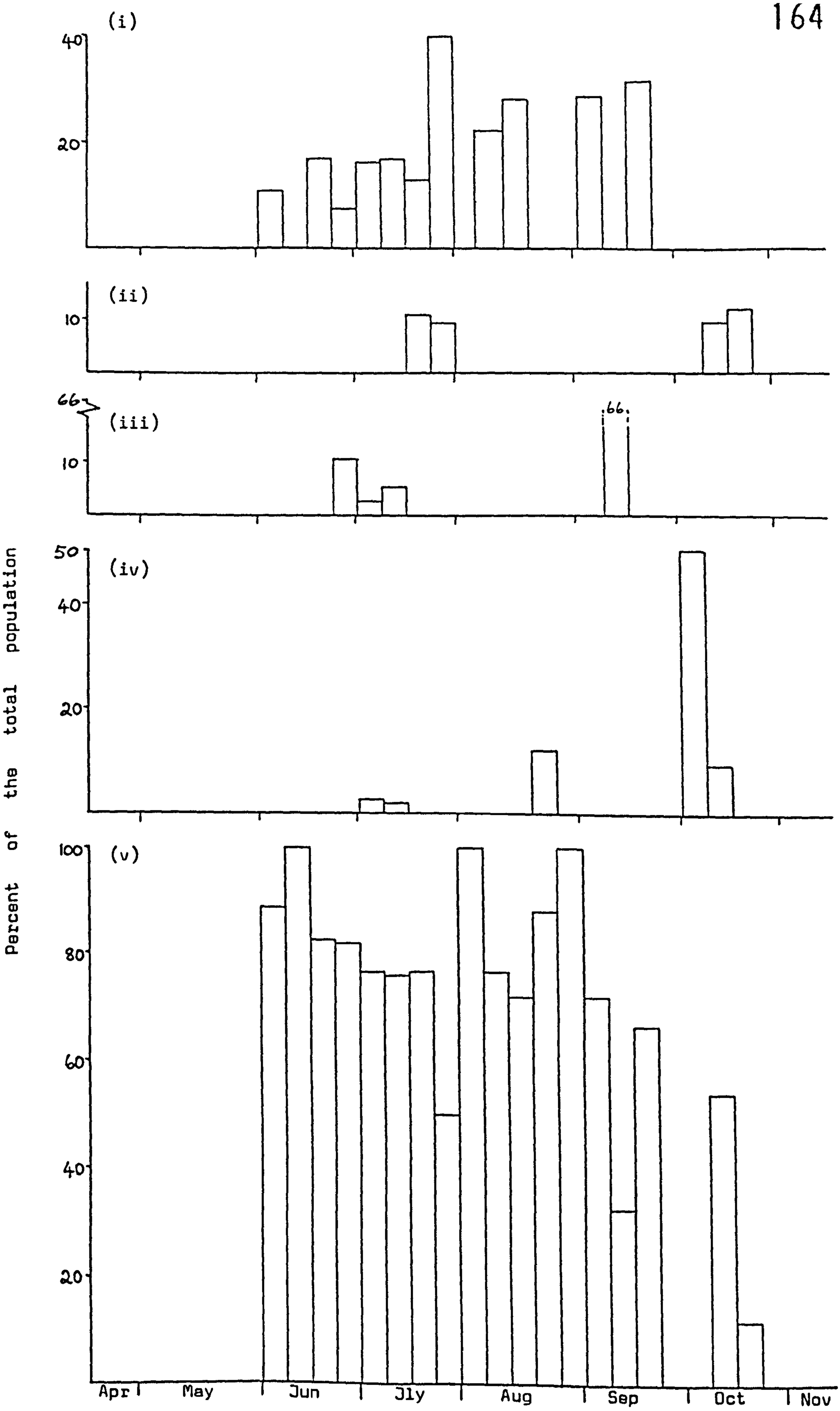
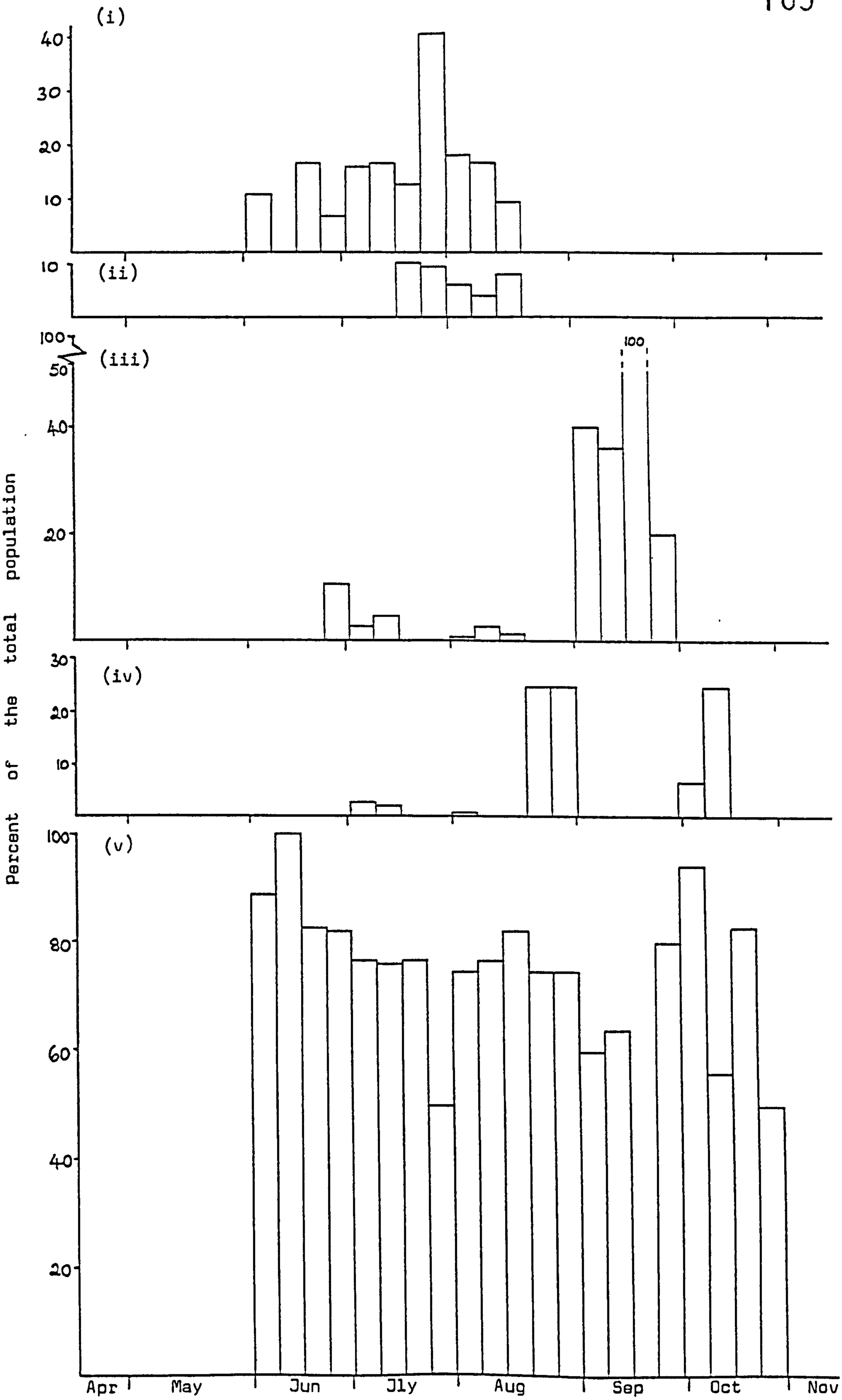

(i)
40
20
(ii)
10
66
(iii)
10
66
(iv)
50
40
20
total population
(v)
100
80
60
40
20
Percent of tha
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 82:

Age structure of the population on WM 109,

Section B, 1982.

For legend, see Figure 81.


(i)
40
30
20
10
(ii)
10
(iii)
100
50
40
20
100
(iv)
30
20
10
(v)
100
80
60
40
20
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

present and thus more of each age class appearing in samples. Males and oviparae were found on both sections during October but peak numbers were low relative to WM110 ($d = -2.18$, $p < 0.05$).

(ii) Spatial distribution of aphids

On the uncut section, the value of b was 1.1 on terminal leaves and 1.25 on non terminals (table 26). These values are significantly different from 1 (for terminals, $t = 2.53$, $p < 0.05$; non terminals, $t=2.83$, $p < 0.01$) but the smaller numbers of aphids present compared to those on other windbreaks, such as WM110 in 1982 or LF125 in 1983 and 1984 may have contributed to the lower b value than for samples on other windbreaks. When the mean and variance are small they become equal or very similar (see fig.8) and it appears that this happened with the samples on this section.

On the pruned section, b for terminal leaves was 1.42 and for non-terminals 1.45 (table 26). These values are significantly different from unity, indicating that the aphids were aggregated over the whole season. The values of Morisita's index of dispersion (table 18) were high when aphids first appeared on the windbreak and fell as the numbers of aphids increased. When aphid numbers were low at the end of the season the value of the index fell to zero as aphids were distributed singly on the leaves.

(iii) Abundance of natural enemies

The only predators recorded were occasional adults of B.angulatus during August. Mummified carcasses of aphids were found infrequently in July and August, but insufficient adults could be found for dissection. All collected mummies produced specimens of T.pallidus.

Table 18 MORISITA'S INDEX OF DISPERSION - WM109, 1982

Date		SECTION A		SECTION B	
		Terminal leaves	Non-terminal leaves	Terminal leaves	Non-terminal leaves
June	3		100.0		86.4
	10		0		0
	17	0	29.1	0	2.8
	24		7.1	0	6.1
July	1		5.2		5.3
	8	0	4.0	0	6.4
	15	0	3.7	0	5.4
	22	16.7	5.2	16.6	6.8
	29	0	0	14.2	7.2
Aug	5	2.8	3.7	2.0	3.2
	12	0	3.4	4.0	2.8
	19	0	2.4	50.0	0
	26	0	0	0	0
Sept	2		10.0		0
	9		0	0	26.8
	16	0	0	0	
	23				0
	30		0	0	16.5
Oct	7	0	2.8	0	1.5
	14	0	0		0
	21	0	0		
	28	0			

2.5.7. WM110, 1983

(i) Abundance of aphids

The section left unpruned during summer 1982 was divided and one half cut in January 1983. Three sections were thus sampled during 1983 and hereafter these will be referred to as

'section 1' - uncut summer 1982, uncut winter 1982/3

'section 2'- uncut summer 1982, cut winter 1982/3

'section 3'- cut summer 1982

Sections 1 and 3 were pruned between July 21st and 28th 1983 and section 2 left untouched.

Aphids hatched in late April on all sections and numbers began to increase with the onset of reproduction by the fundatrices in late May (figs.83,84,85). Fundatrices were more common on section 3 than section 1 ($d=2.54$, $p<0.05$) or section 2 ($d=2.03$, $p<0.05$). Numbers on section 1 were similar to those on section 2 ($d=0.54$, $p>0.05$). Populations increased rapidly during June and numbers peaked on July 14th (section 3) and July 21st (sections 1 and 2). The maximum attained was similar on section 1 and 2 but considerably greater than that on section 3 (table 19). Numbers declined sharply and there were small resurgences in September and October. The pattern of abundance on terminal and non-terminal leaves followed similar trends to the total population (figs.83b,84b,85b) with more aphids present on the non terminal leaves. Pruning took place after the populations had peaked. On section 3 aphid numbers were already declining and beginning to do so on section 1. On section 2, the uncut part, numbers on the sampling date after pruning (of the other sections) were 25% of what they were before. On section 1 the figure was 15% and on section 3, 30%. If it is assumed that section 2 is the 'control' section then it appears that aphid numbers were reduced on section 1 ($d=16.71$, $p<0.001$) but were greater

Figure 83:

Aphid populations on WM 110, section 1, 1983

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

Arrow represents date of pruning

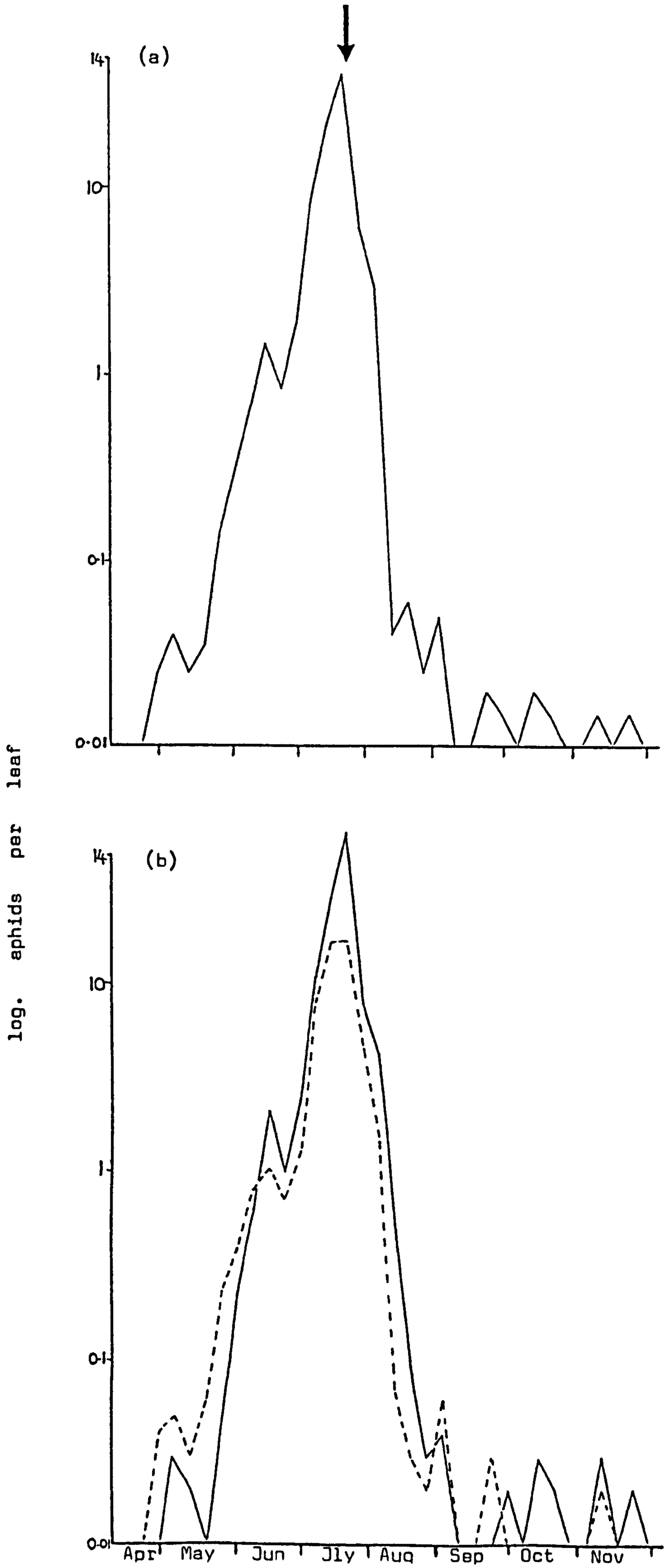

(a)
14
10
1
0·1
0·01
(b)
10
1
0·1
0·01
log. aphids per leaf
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 84:

Aphid populations on WM 110,section 2,1983

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

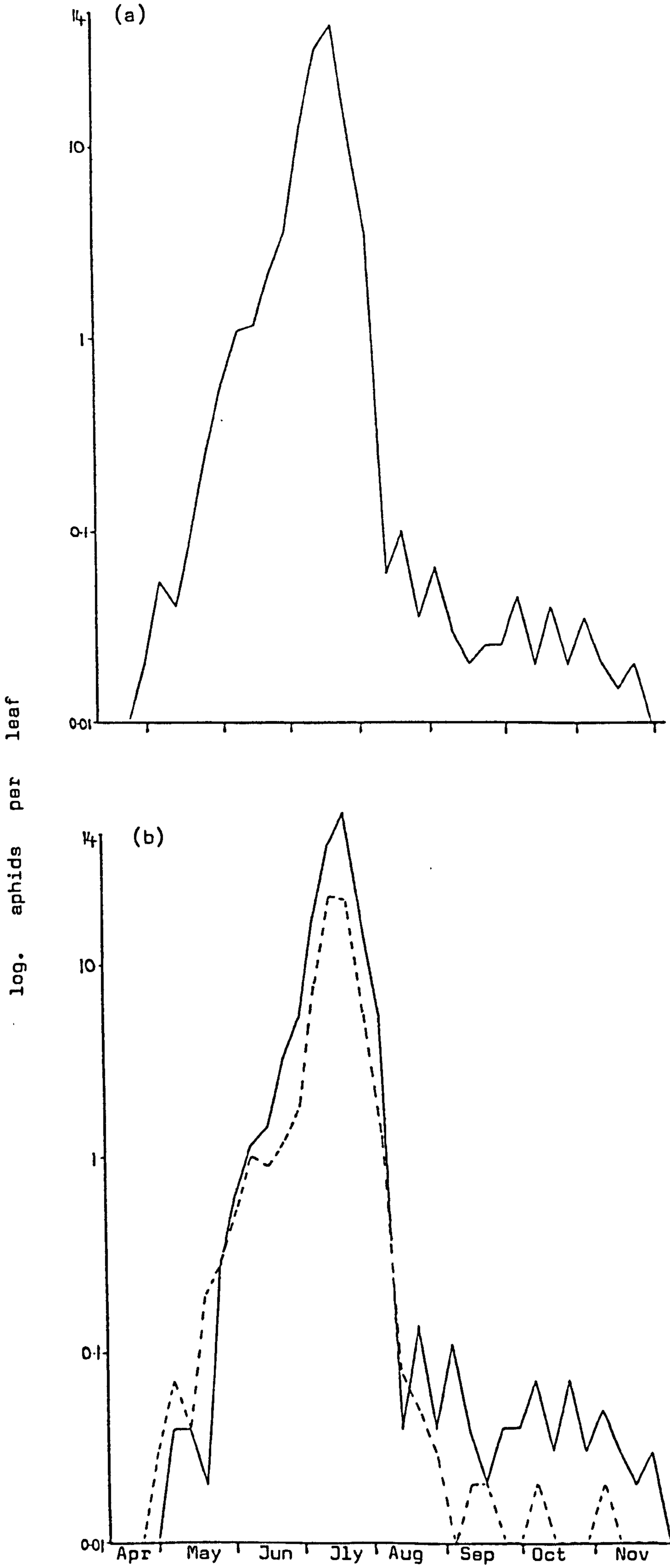

(a)
14
10
1
0·1
0·01
(b)
14
10
1
0·1
0·01
log. aphids per leaf
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 85:

Aphid populations on WM 110,section 3, 1983

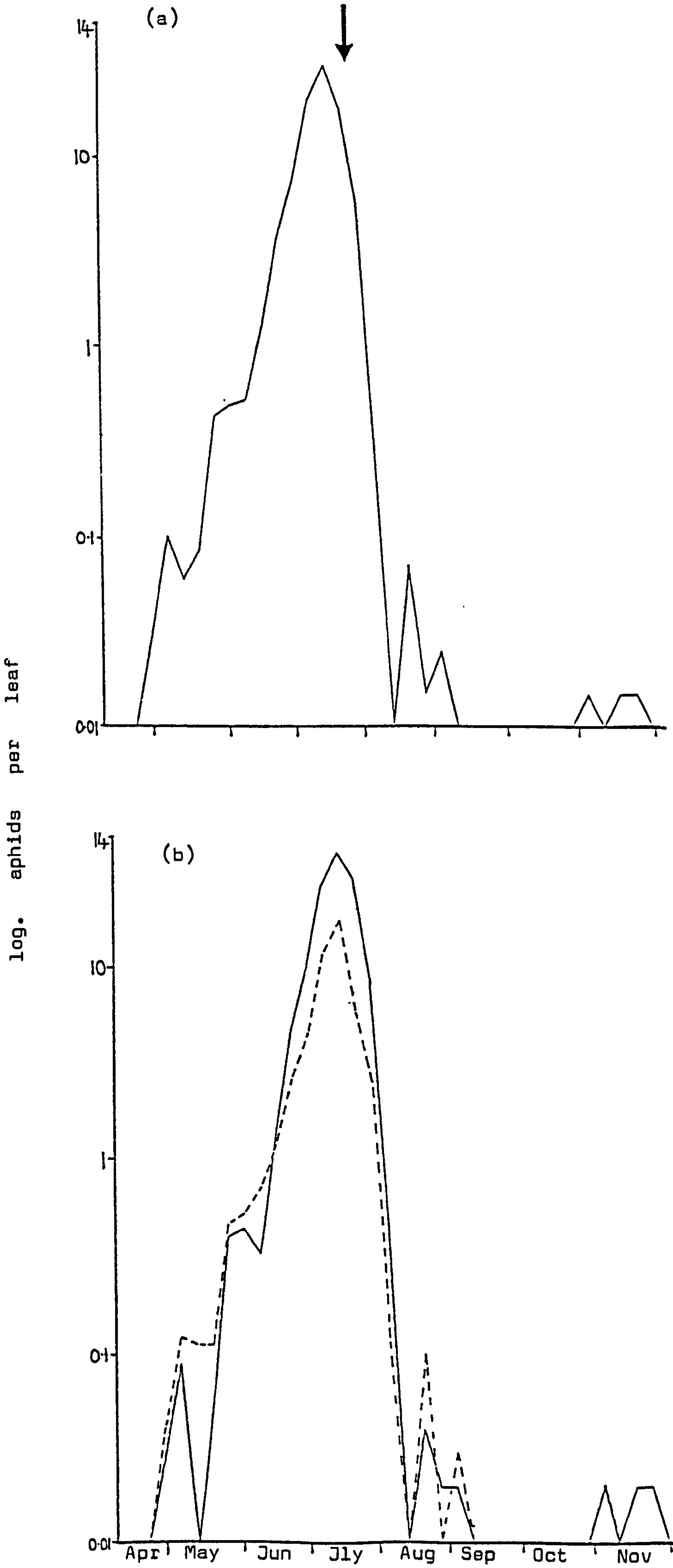
(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

Arros represents date of pruning


(a)
14
10
1
0·1
0·01
(b)
14
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov
log. aphids per leaf

relative to the previous week's numbers on section 3 ($d=5.79$, $p<0.001$). When aphid numbers were near their peak, pruning thus appeared to have the same effect on reduction as in 1982. However when aphid numbers were declining the effect was less clear.

As with other windbreaks previously mentioned, the population density was greatest on terminal leaves throughout the period of population increase (fig.86a,b,c,). When pruning took place the pattern was reversed, due to the terminal leaves on a twig no longer being the youngest leaves. Leaves which previously had been non terminal, became terminal when pruning occurred and the aphids appeared to redistribute themselves over the leaves. This phenomenon did not occur at a similar time on section 2 but happened later in the season.

The age structure of the populations indicated that instars I-III accounted for 70-90% of total numbers during the period of population increase (figs.87,88,89). When the numbers began to decline, this proportion fell and populations in early August contained 50% nymphs and 50% alate adults, on all sections. Alate adults had disappeared by early September and subsequently the nymphal proportion fluctuated widely between 0 and 100%, with variable proportions of apterous adults. Proportions were variable due to the low numbers of aphids present (table 19). The age structure of the populations was different on terminal and non terminal leaves (appendix 2.6, 2.7, 2.8). Proportions of fourth instars (presumptive alatae) were greater on terminals and that of alate adults greatest on non terminals during the period of population increase.

Alate adults were recorded on each section before alate fourth instars were found. As occurred in 1982 this may have been due to the sampling procedure not being sensitive enough to record the fourth instars or the arrival of adults from other alder. Potential alatae appeared in mid June

Figure 86:

Population density of <u>P.alni</u> on WM 110, 1983

(a) Section 1

(b) Section 2

(c) Section 3

- - - - Terminal leaves

——— Non-terminal leaves

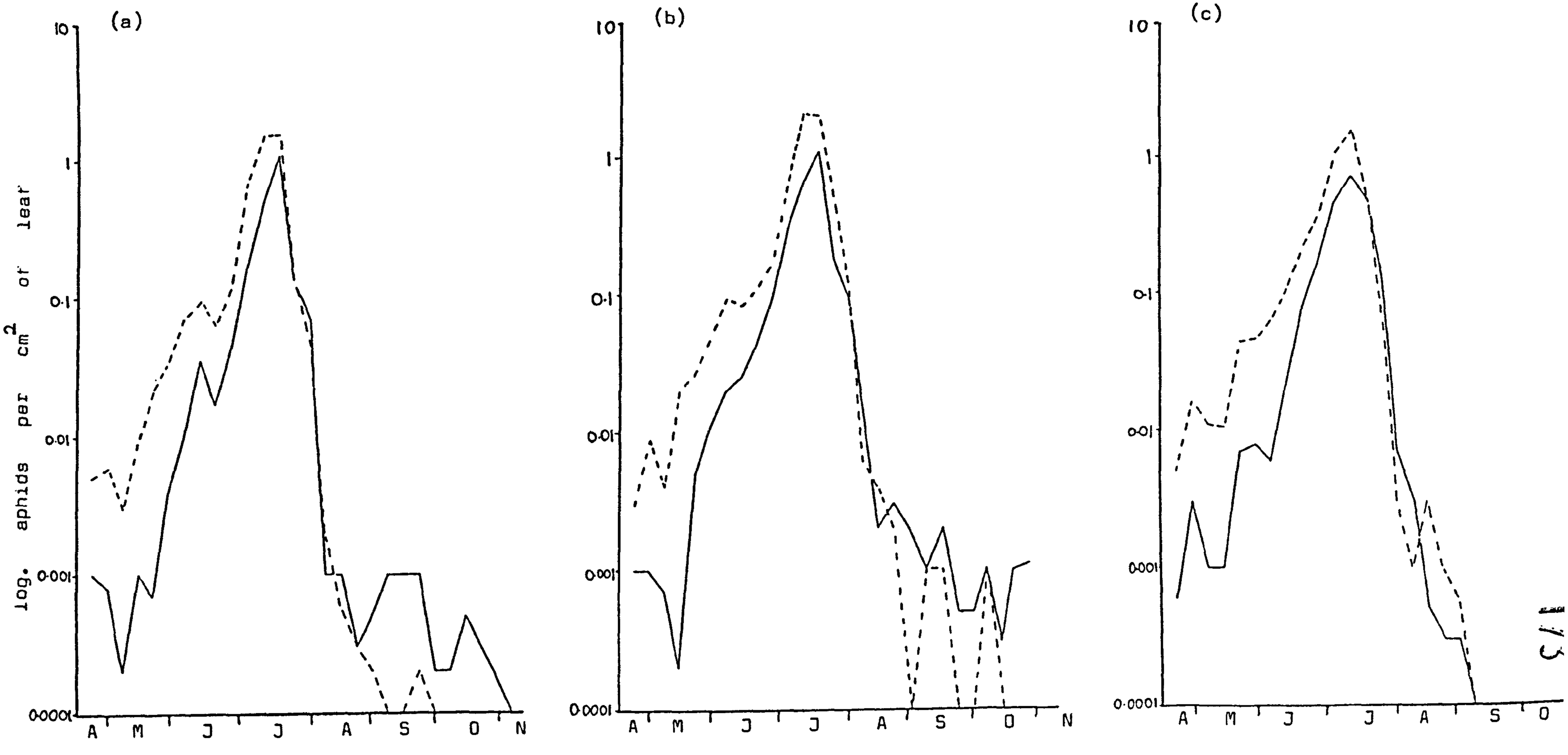

(a)
(b)
(c)
10
1
0·1
0·01
0·001
0·0001
log. aphids per cm² of leaf
A M J J A S O N
A M J J A S O N
A M J J A S O

Figure 87:

Age structure of the population on WM.110,

section 1, 1983

(i) Alate adults

(ii) Fourth instars (presumptive alatae)

(iii) Apterous adults

(iv) Fourth instars (presumptive apterae)

(v) Nymphs

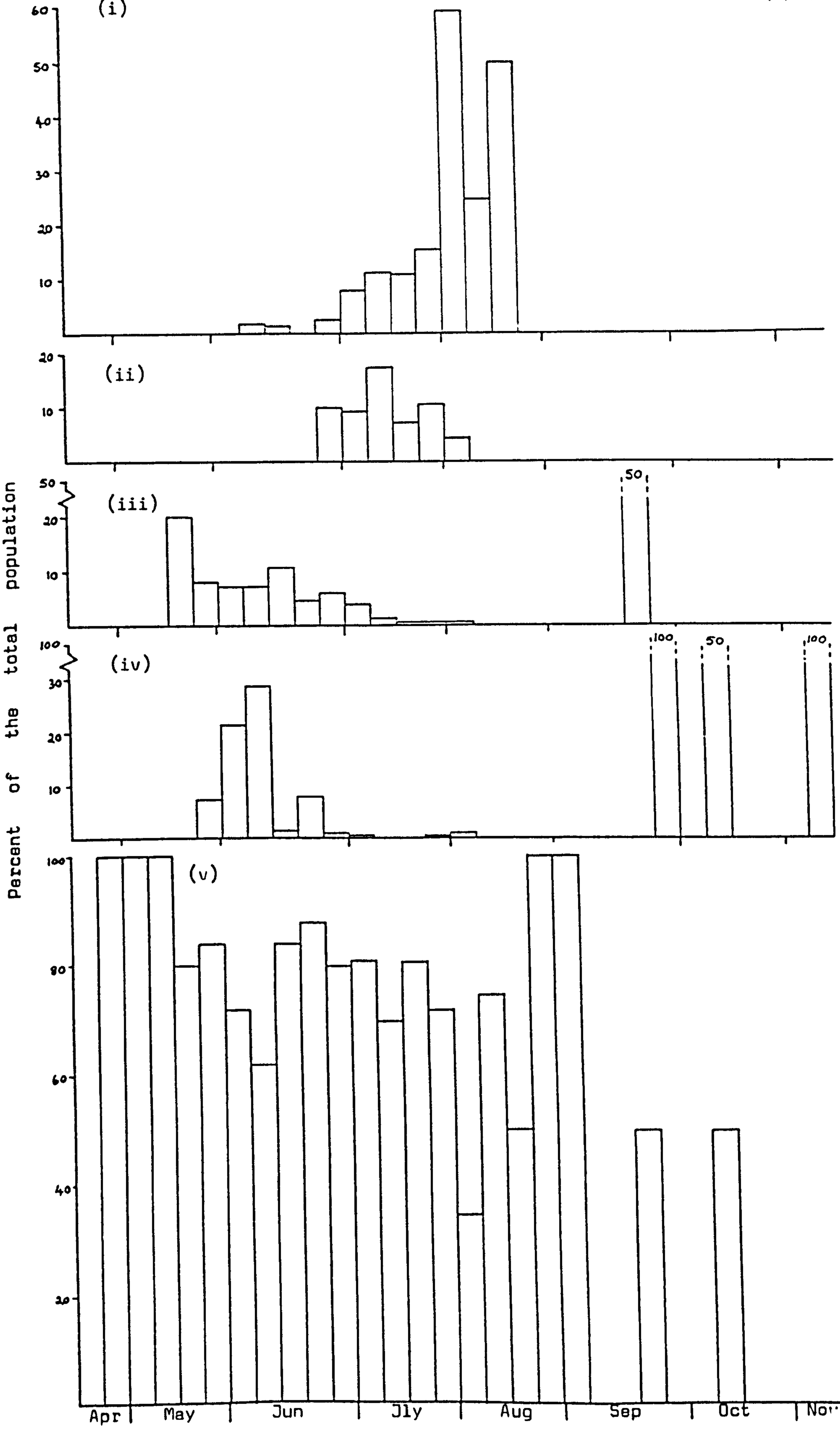

(i)
60
50
40
30
20
10
(ii)
20
10
(iii)
50
20
10
50
(iv)
100
30
20
10
100
50
100
(v)
100
80
60
40
20
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 88:

Age structure of the population on WM 110

Section 2, 1983

For legend, see figure 87

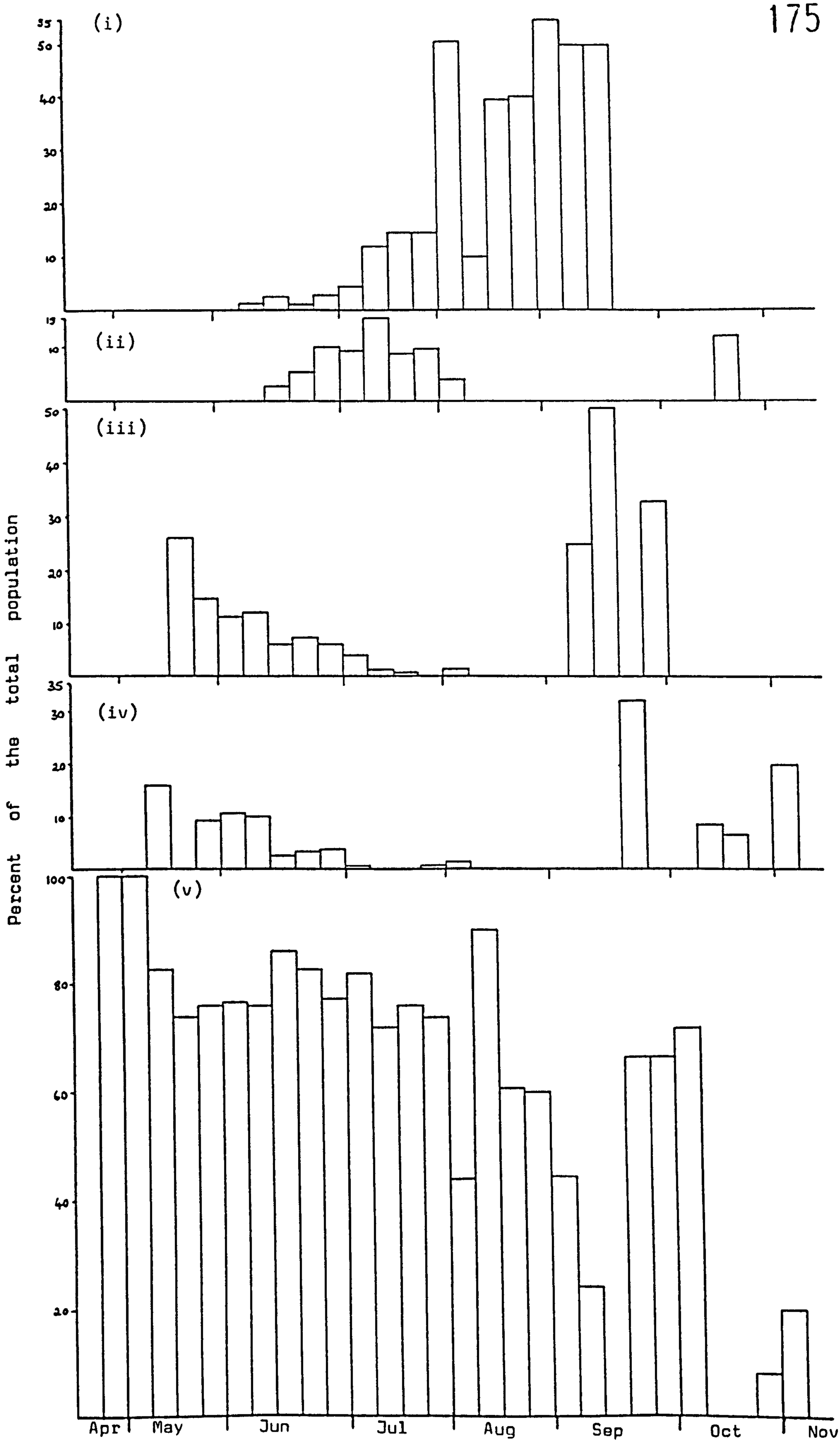

(i)
55
50
40
30
20
10
(ii)
15
10
(iii)
50
40
30
20
10
(iv)
35
30
20
10
(v)
100
80
60
40
20
Percent of the total population
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Figure 89:

Age structure of the population on WM110

section 3, 1983

For legend, see figure 87.

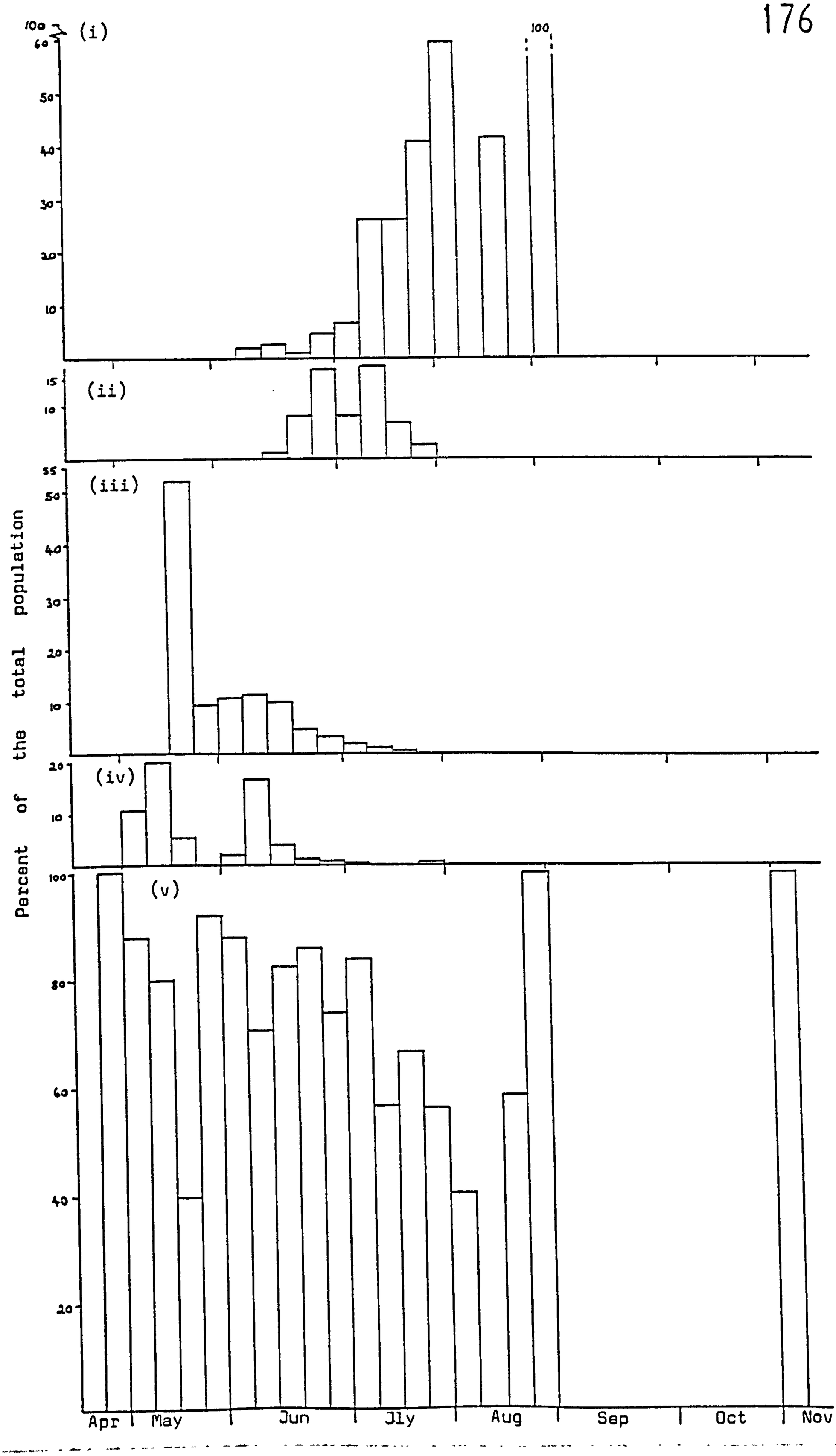

(i)
100
60
50
40
30
20
10
100
(ii)
15
10
(iii)
55
50
40
30
20
10
Percent of the total population
(iv)
20
10
(v)
100
80
60
40
20
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Table 19 TOTAL NUMBERS OF APHIDS IN LEAF SAMPLES - WM110, 1983

		SECTION 1			SECTION 2			SECTION 3		
Date		Aphids/ 100 Terminal leaves	Aphids/ 100 Non-terminal leaves	Aphids/ Whole sample	Aphids/ 100 Terminal leaves	Aphids/ 100 Non-terminal leaves	Aphids/ Whole sample	Aphids/ 100 Terminal leaves	Aphids/ 100 Non-terminal leaves	Aphids/ Whole sample
April	28	3	0	3	2	0	2	3	1	4
May	5	4	2	6	5	3	8	11	7	18
	12	2	1	3	3	3	6	10	0	10
	19	5	0	5	18	1	19	10	5	15
	26	22	4	26	27	27	54	45	39	84
June	2	38	22	60	53	65	118	52	44	96
	9	77	58	135	102	118	220	70	32	103
	16	102	210	312	91	147	238	118	133	251
	23	69	97	166	123	321	444	259	471	730
	30	128	249	377	186	532	718	449	998	1447
July	7	745	1007	1752	757	1801	2558	1150	2740	3890
	14	1655	2926	4581	2363	4484	6847	1725	4147	5872
	21	1696	6617	8313	2240	6520	8760	596	2957	3553
	28	469	787	1256	561	1666	2227	251	834	1085
Aug	4	154	417	571	133	552	685	11	43	54
	11	6	6	12	7	3	10	0	0	0
	18	2	8	10	4	14	18	9	3	12
	25	1	2	3	2	3	5	0	1	1
Sept	1	5	3	8	0	11	11	2	1	3
	8	0	0	0	1	3	4	0	0	0
	15	0	0	0	1	1	2	0	0	0
	22	2	0	2	0	3	3	0	0	0
	29	0	1	1	0	3	3	0	0	0
Oct	6	0	0	0	1	6	7	0	0	0
	13	0	2	2	0	2	2	0	0	0
	20	0	1	1	0	6	6	0	0	0
	27	0	0	0	0	2	2	0	0	0
Nov	3	0	0	0	1	4	5	1	1	2
	10	1	2	3	0	2	2	0	0	0
	17	0	0	0	0	1	1	0	1	1
	24	0	1	1	0	2	2	0	1	1

on sections 2 and 3 and 2 weeks later on section 1. Numbers rapidly increased and at the time of the population peaks the fourth instar was entirely presumptive alatae. No alate adults appeared to be produced after the first week in August (fig.90).

Alate adults were produced in the third generation on each section, the first two generations being apterous. The third and fourth generations were entirely alate, the fifth and sixth apterous and the seventh, last generation was the sexual forms.

Males first appeared in early October, but were only found on section 2. Their appearance preceded that of oviparae (fig.91). Ovipara numbers were low (fig.91b,d,f,) and they were less common than on the corresponding sections in 1982 (section 1, $d= -2.96$, $p < 0.01$; section 2, $d=-2.18$, $p < 0.05$; section 3, $d= -3.21$, $p < 0.01$).

(ii) Spatial distribution of aphids

All values of b on terminal and non terminal leaves for each section were significantly different from unity (table 26) indicating that the aphids were aggregated over the season. The values of Morisita's index (table 20) followed a similar pattern to those described for LF125 and WM110 in 1982. Values indicated that the aphids were aggregated at the beginning of the season and after the decline in numbers. During the period of population increase the index decreased as more leaves were colonized.

(iii) Abundance of natural enemies

Predator numbers were similar on sections 1 and 2 ($t=0.68$, d.f.$=52$, $p > 0.05$) but they were commoner on section 3, than on 1 ($d=2.29$, d.f.$=30$, $p < 0.05$) or 2 ($d=2.04$, d.f.$=33$, $p < 0.05$). Total numbers throughout the season are shown in fig.92a.c.e. Pruning did not appear to affect predator numbers on section 1 and numbers did not decline at a similar time on section 2.

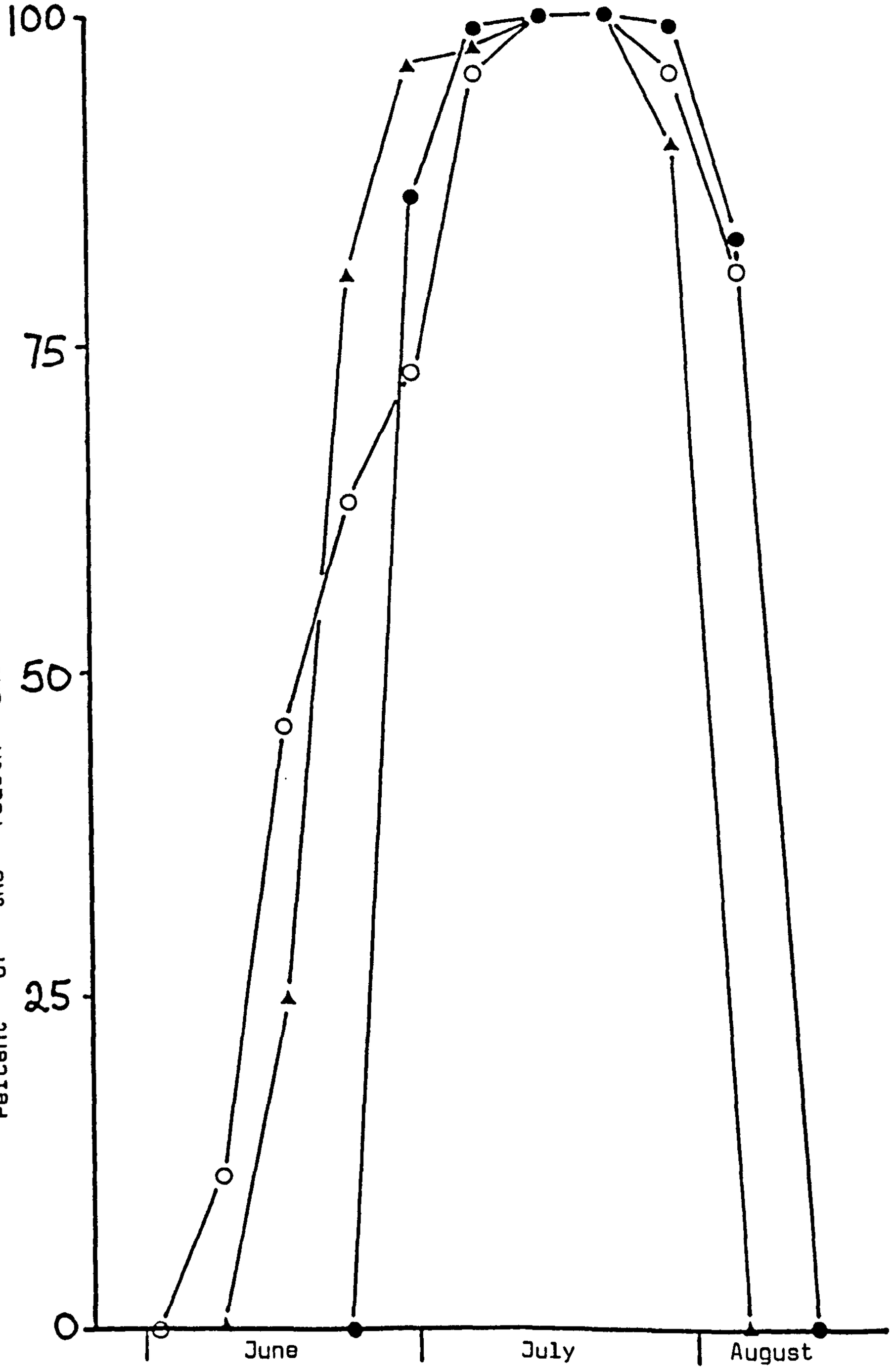


Figure 90: Proportion of presumptive alatae in the fourth instar, WM 110, 1983.

Figure 91:

Abundance of sexuales on WM 110 1983

(a) Appearance of sexuales, section 1

(b) Numbers of oviparae, section 1

(c) Appearance of sexuales, section 2

(d) Numbers of oviparae, section 2

(e) Appearance of sexuales, section 3

(f) Numbers of oviparae, section 3

Males

Oviparae

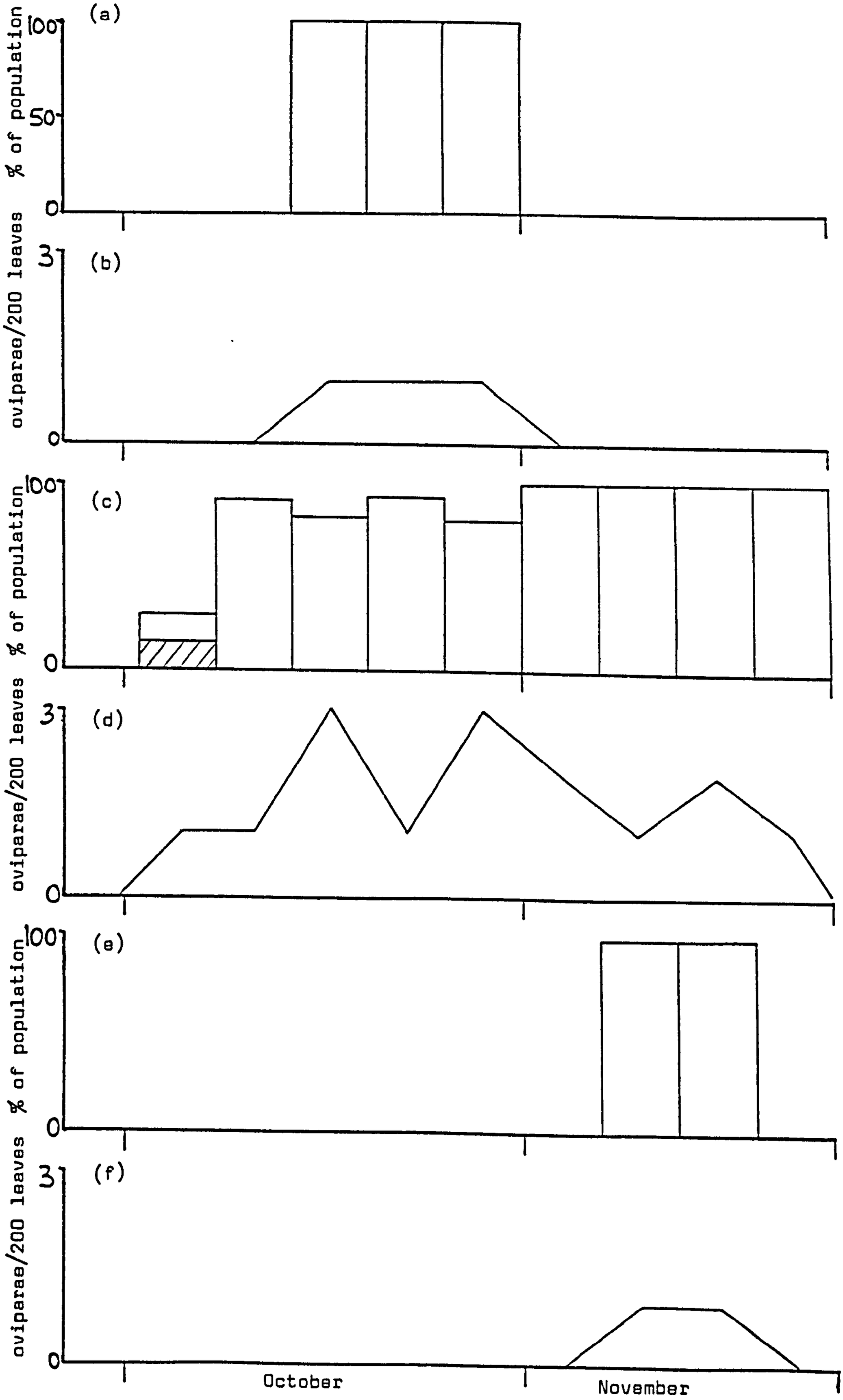

(a)
100
50
0
% of population
(b)
3
0
oviparae/200 leaves
(c)
100
0
% of population
(d)
3
0
oviparae/200 leaves
(e)
100
0
% of population
(f)
3
0
oviparae/200 leaves
October
November

Table 20 MORISITA'S INDEX OF DISPERSION - WM110, 1983

Date		SECTION 1		SECTION 2		SECTION 3	
		Terminal leaves	Non-terminal leaves	Terminal leaves	Non-terminal leaves	Terminal leaves	Non-terminal leaves
May	5	0	0	6.7	0	5.5	10.0
	12	0	0	0	0	8.9	
	19	0		88.9	0	15.6	10.0
	26	23.6	0	50.2	30.6	15.7	29.8
June	2	12.2	12.6	14.7	18.4	10.6	9.2
	9	9.3	30.2	9.3	15.4	9.4	76.8
	16	8.8	14.1	6.7	10.1	16.0	9.1
	23	21.7	9.8	12.3	14.8	15.5	8.9
	30	15.9	6.6	18.1	6.3	8.3	16.9
July	7	4.5	5.7	4.4	2.5	3.4	2.1
	14	2.9	1.8	2.5	2.1	2.4	1.5
	21	2.7	2.2	2.5	2.1	3.7	2.2
	28	2.2	4.0	2.6	2.7	3.1	3.0
Aug	4	3.4	2.0	4.0	2.0	16.4	3.5
	11	20.0	6.7	4.8	100.0		
	18	100.0	14.2	50.0	3.3	11.1	0
	25	0	0	0	33.3		0
Sept	1	0	33.3		5.5	0	0
	8			0	0		
	15			0	0		
	22	0			0		
	29	0	0		100.0		
Oct	6			0	6.7		
	13		0		0		
	20		0		0		
	27				0		
Nov	3			0	16.7	0	0
	10	0	100.0		0		
	17				0		0
	24		0		0		0

Figure 92:

Abundance of predators, WM 110, 1983

(a) Total numbers, section 1

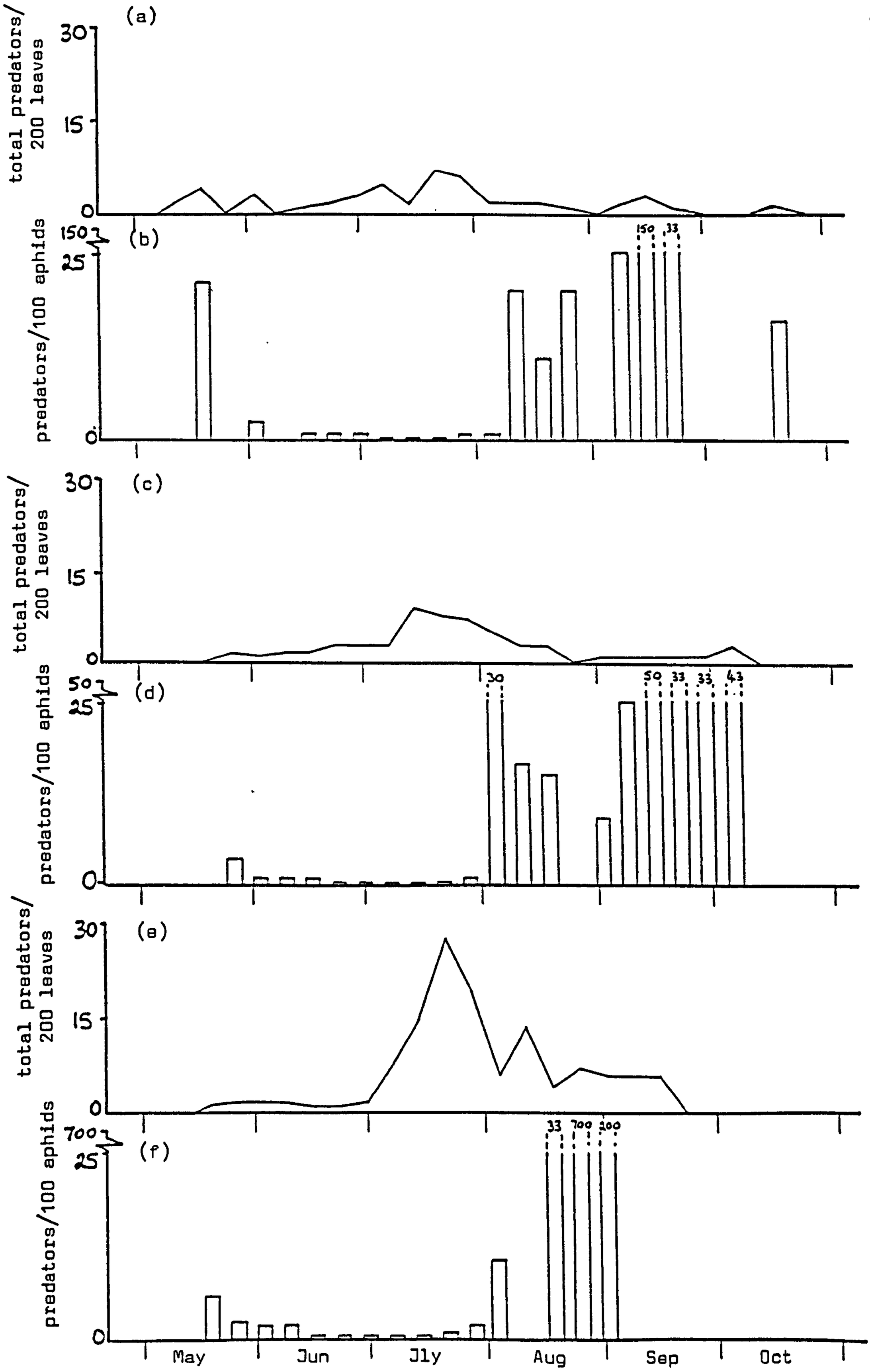
(b) Ratio of predators to aphids,section 1

(c) Total numbers, section 2

(d) Ratio of predators to aphids,section 2

(e) Total numbers, section 3

(f) Ratio of predators to aphids,section 3


(a)
total predators/ 200 leaves
30
15
0
(b)
predators/100 aphids
150
25
0
150
33
(c)
total predators/ 200 leaves
30
15
0
(d)
predators/100 aphids
50
25
0
36
50
33
33
43
(e)
total predators/ 200 leaves
30
15
0
(f)
predators/100 aphids
700
25
0
33
700
100
May
Jun
Jly
Aug
Sep
Oct

Numbers declined sharply on section 3 subsequent to pruning. At this time B.angulatus comprised 85% of predator numbers. Although the number of adults found increased, nymphs decreased. The bugs were becoming adult at this time and the reduction in numbers may have been due to loss of nymphs or migration of adults as they became mature. Nymphs may still hatch from the egg at this time and as sticky traps placed near the windbreak did not record an increase in adult bugs trapped until later in the season (chapter 3) it seems likely that the drop in predator numbers was due to loss of nymphs.

The ratio of predators to aphids fell during the period of aphid population increase (fig.92);on section 1 where predators were least numerous there was 1 per 1200 aphids at the time of the aphid population peak and this rose to 1.5 per aphid in mid September. At the population peaks on sections 2 and 3 there was 1 per 1000 aphids and 3 per 1000 respectively. The ratio rose to 1 to every 2 aphids on section 2 and to 7 per aphid on section 3 in early September.

The only coccinellid found was A.bipunctata and A.nemorum the only anthocorid. No examples of P.ambiguus were found on sections 2 or 3 and O.marginalis was recorded in small numbers on each section. Syrphid larvae were the second commonest predators on each section and on section 2 accounted for 28% of total numbers. Larvae of S.ribesii and E.balteatus were recorded, the former being more common. The most abundant predator was B.angulatus comprising 61% of total numbers on section 1, 48% on section 2 and 82% on section 3 (fig.93). Nymphs appeared in mid June and adults in late July; females persisted until late September (fig.94). Small numbers of larvae of C.carnea and A.aphidimyza were found on each section.

Parasitism by T.pallidus was first observed in late June (fig.95). The

Figure 93:

Relative abundance of predators, WM 110, 1983

(a) Section 1

(b) Section 2

(c) Section 3

(1) Coccinellidae

(2) Anthocoridae

(3) B.angulatus

(4) O.marginalis

(5) P.ambiguus

(6) Neuroptera

(7) Syrphidae

(8) Cecidomyiidae

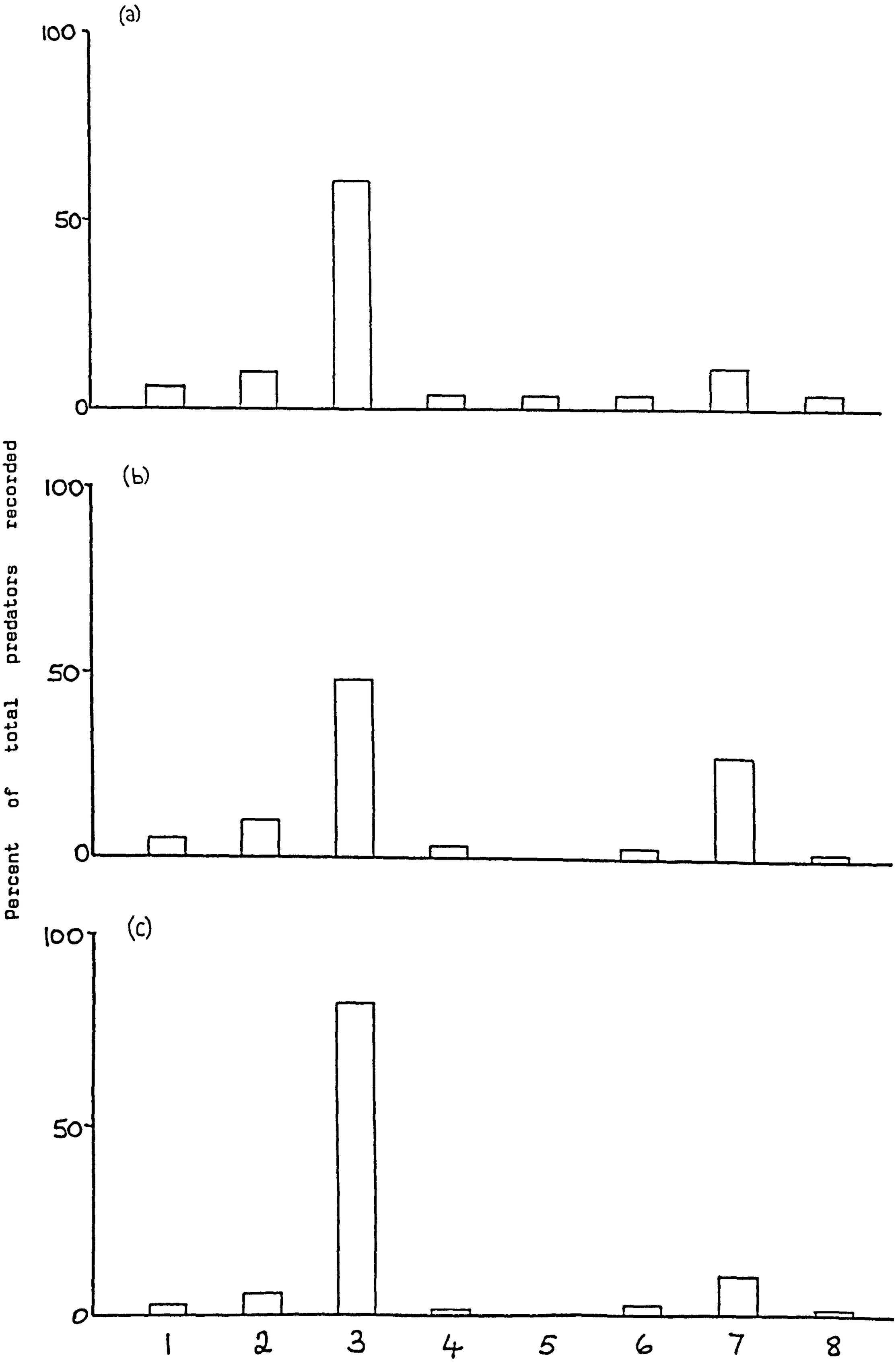

(a)
100
50
0
(b)
100
50
0
Percent of total predators recorded
(c)
100
50
0
1
2
3
4
5
6
7
8

Figure 94:

Numbers of B.angulatus on WM 110, 1983

(a) Section 1 — Nymphs

(b) Section 2 — Males

(c) Section 3 — Females

Figure 95:

Parasitism and fungal disease in populations of P.alni, WM 110, 1983

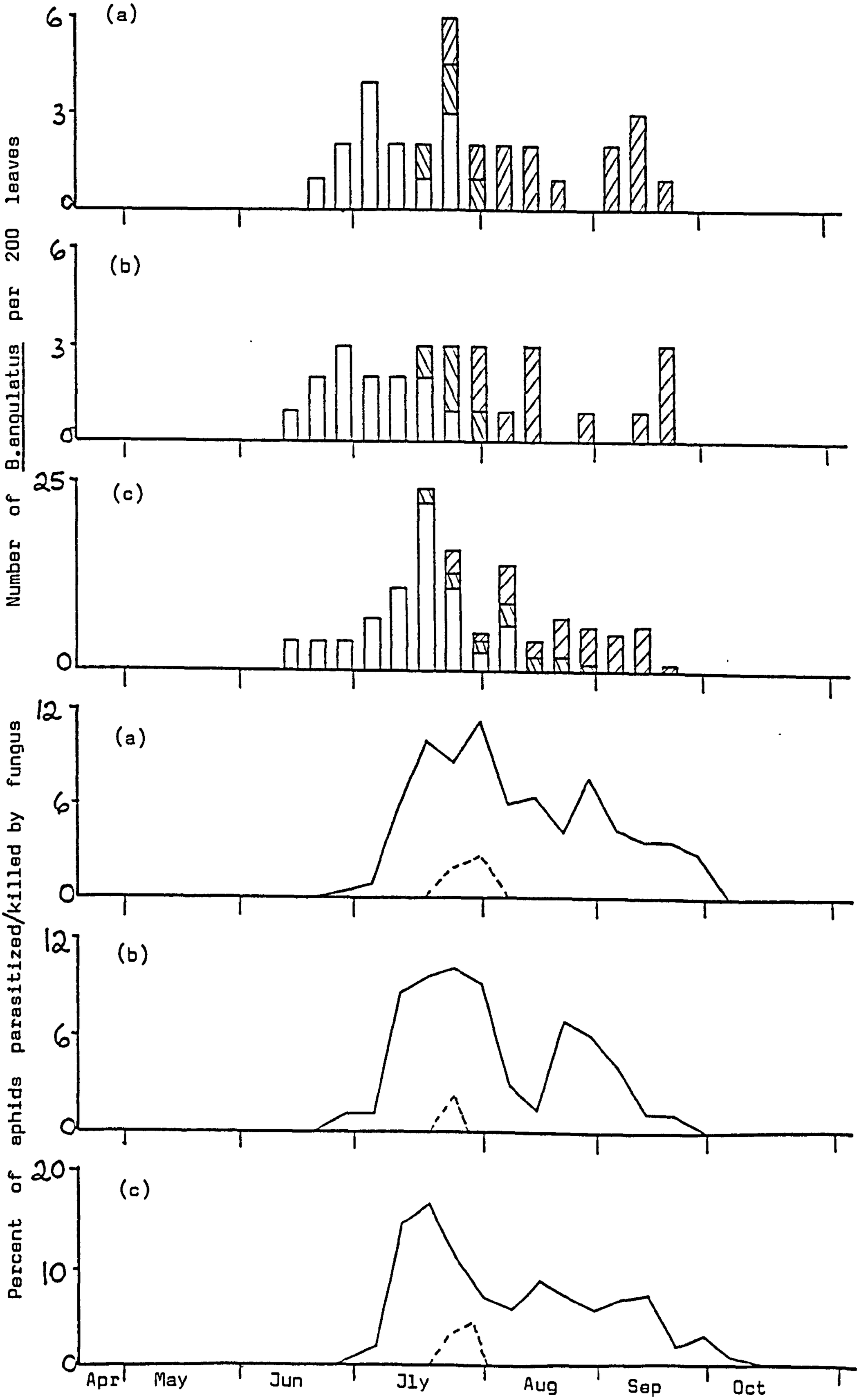
(a) Section 1

(b) Section 2

(c) Section 3

_____ parasitism

- - - Entomophthora


Number of B.angulatus per 20 leaves
(a)
6
3
0
(b)
6
3
0
(c)
25
0
aphids parasitized/killed by fungus
(a)
12
6
0
(b)
12
6
0
Percent of
(c)
20
10
0
Apr
May
Jun
Jly
Aug
Sep
Oct

percentage of adults parasitized was similar on all sections reaching a maximum of 10.0% on section 1, 11.1% on section 2 and 16.7% on section 3 (sections 1 and 2, d=0.19, $p > 0.05$; sections 1 and 3, d=1.01, $p > 0.05$; sections 2 and 3, d=0.89, $p > 0.05$). Isolated examples of aphids killed by E.occidentalis were found in late July (fig.95).

2.5.8 WM109, 1983

(i) Abundance of aphids

Both sections were cut between July 25th and August 1st. The section which was cut in summer 1982 and which was to the north of WM110 (see fig.1b) will hereafter be referred to as 'section A' and the southern section as 'section B'.

In late April newly hatched nymphs were found on section A on the very small leaves. Only a very small number of buds had begun to burst and no aphids could be found on the unopened buds. No aphids were found after May 2nd until alate adults appeared in mid June. Numbers increased rapidly on both sections (figs.96,97). The pattern of abundance on terminal and non terminal leaves was similar, with more aphids present on the non-terminals. Numbers were considerably less than on WM110 (table 21) and appeared to be reinforced by arriving alates and their subsequent reproduction.

Throughout the period of abundance the population consisted mainly of alate adults and nymphs of instars I-III (figs.98,99), with varying proportions of each. The fluctuation in proportions is a likely result of alate arrival and their reproduction. The offspring produced by the alates grew up as a generation of mostly apterous adults although some alates were produced on section A (fig.98). Very few adults were produced and the population declined rapidly when alate arrivals ceased. No sexual forms

Figure 96:

Aphid populations on WM 109, Section A,1983

(a) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

(b) 200 leaf sample

Arrow represents date of pruning

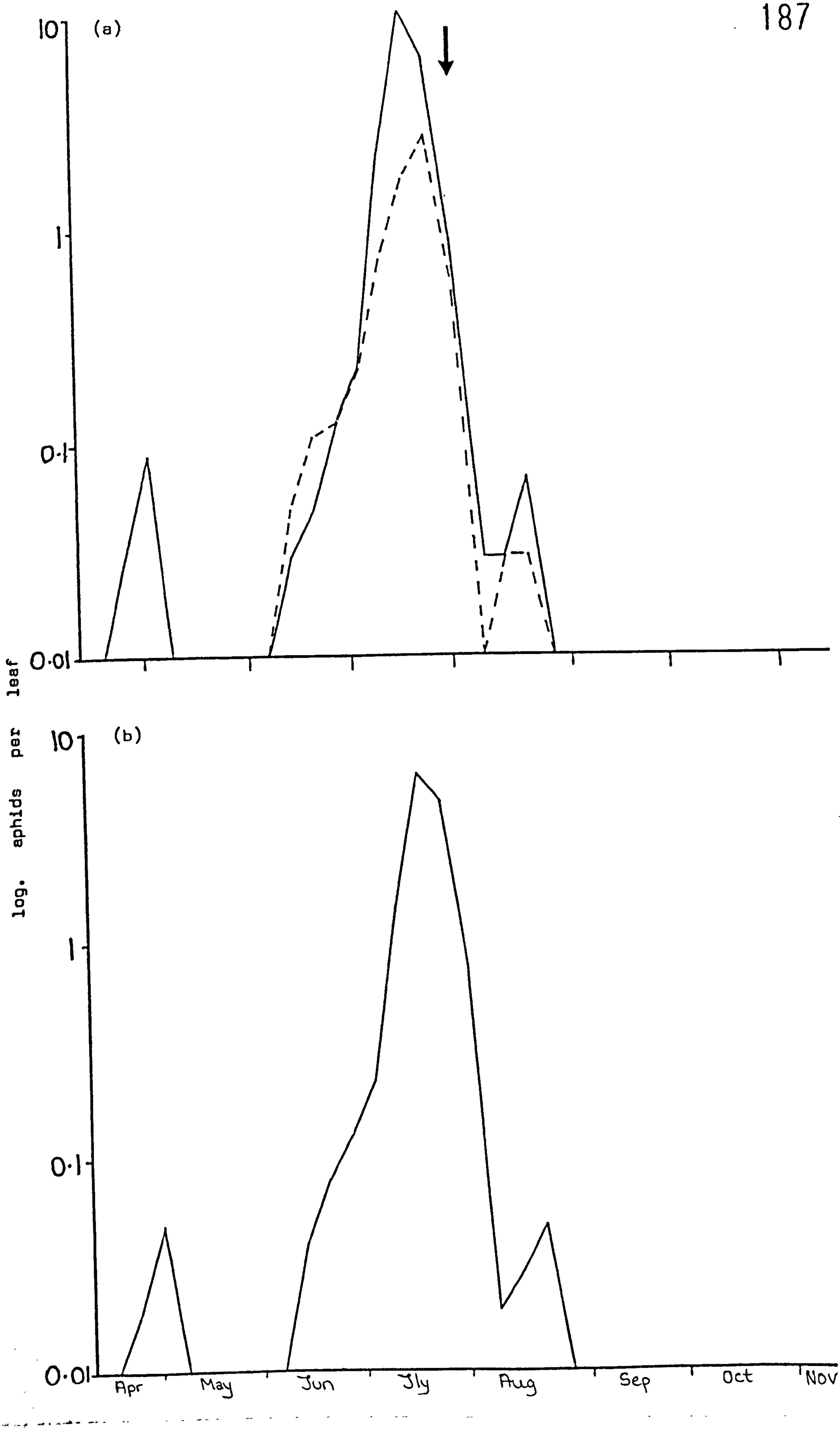

(a)
10
1
0·1
0·01
leaf
log. aphids per
(b)
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 97:

Aphid populations on WM 109, section 8,1983

(a) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

(b) 200 leaf sample

Arrow represents date of pruning

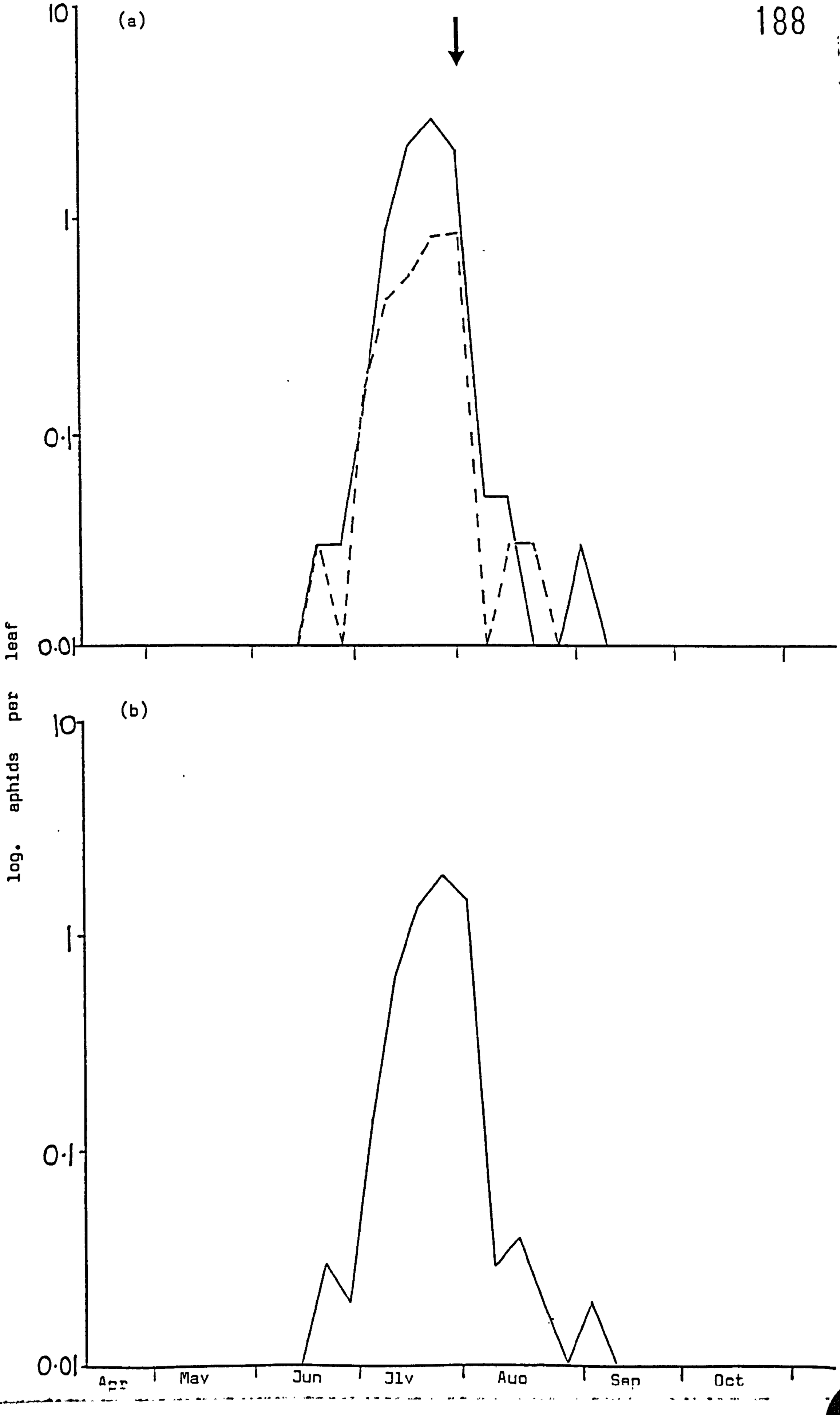

(a)
10
1
0·1
0·01
(b)
10
1
0·1
0·01
log. aphids per leaf
Apr
May
Jun
Jly
Aug
Sep
Oct

Table 21 TOTAL NUMBER OF APHIDS IN LEAF SAMPLES - WM109, 1983

		S E C T I O N A			S E C T I O N B		
Date		Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample	Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample
April	25	0	1	1	0	0	0
May	2	0	4	4	0	0	0
	9	0	0	0	0	0	0
	16	0	0	0	0	0	0
	23	0	0	0	0	0	0
	30	0	0	0	0	0	0
June	6	0	0	0	0	0	0
	13	2	1	3	0	0	0
	20	5	2	7	1	1	2
	27	6	6	12	0	1	1
July	4	11	11	22	7	6	13
	11	37	111	148	21	44	65
	18	86	545	631	28	111	139
	25	138	327	465	41	148	189
Aug	1	30	45	75	43	103	146
	8	0	1	1	0	2	2
	15	1	1	2	1	2	3
	22	1	3	4	1	0	1
	29	0	0	0	0	0	0
Sept	5	0	0	0	0	1	1
	12	0	0	0	0	0	0
	19	0	0	0	0	0	0
	26	0	0	0	0	0	0
Oct	3	0	0	0	0	0	0
	10	0	0	0	0	0	0
	17	0	0	0	0	0	0
	24	0	0	0	0	0	0
	31	0	0	0	0	0	0
Nov	7	0	0	0	0	0	0
	14	0	0	0	0	0	0
	25	0	0	0	0	0	0

Figure 98:

Age structure of the population on WM 109,

Section A, 1983

(i) Alate adults

(ii) Fourth instars (presumptive alatae)

(iii) Apterous adults

(iv) Fourth instars (presumptive apterae)

(v) Nymphs

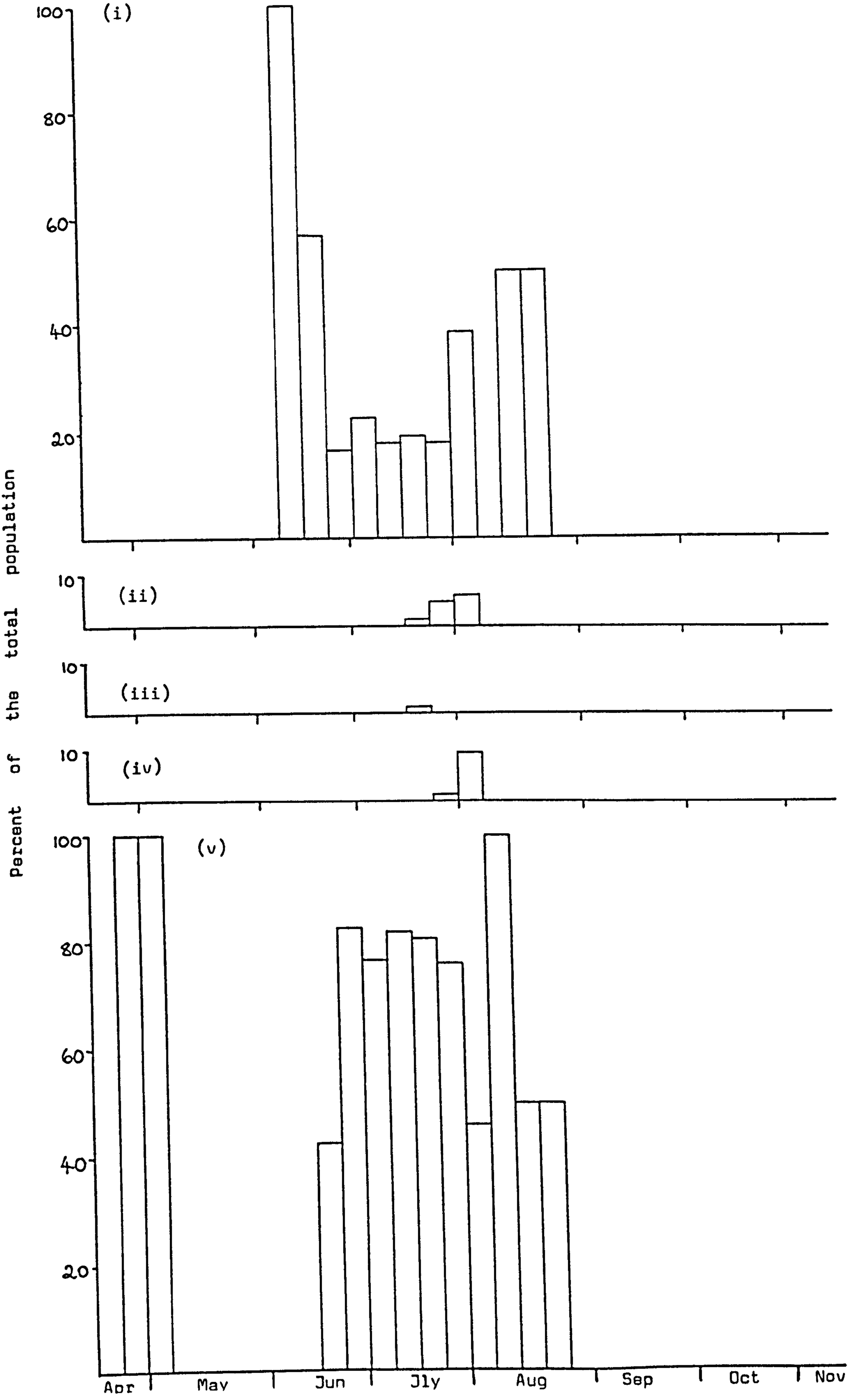

(i)
100
80
60
40
20
(ii)
10
(iii)
10
(iv)
10
(v)
100
80
60
40
20
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 99:

Age structure of the population on WM 109,

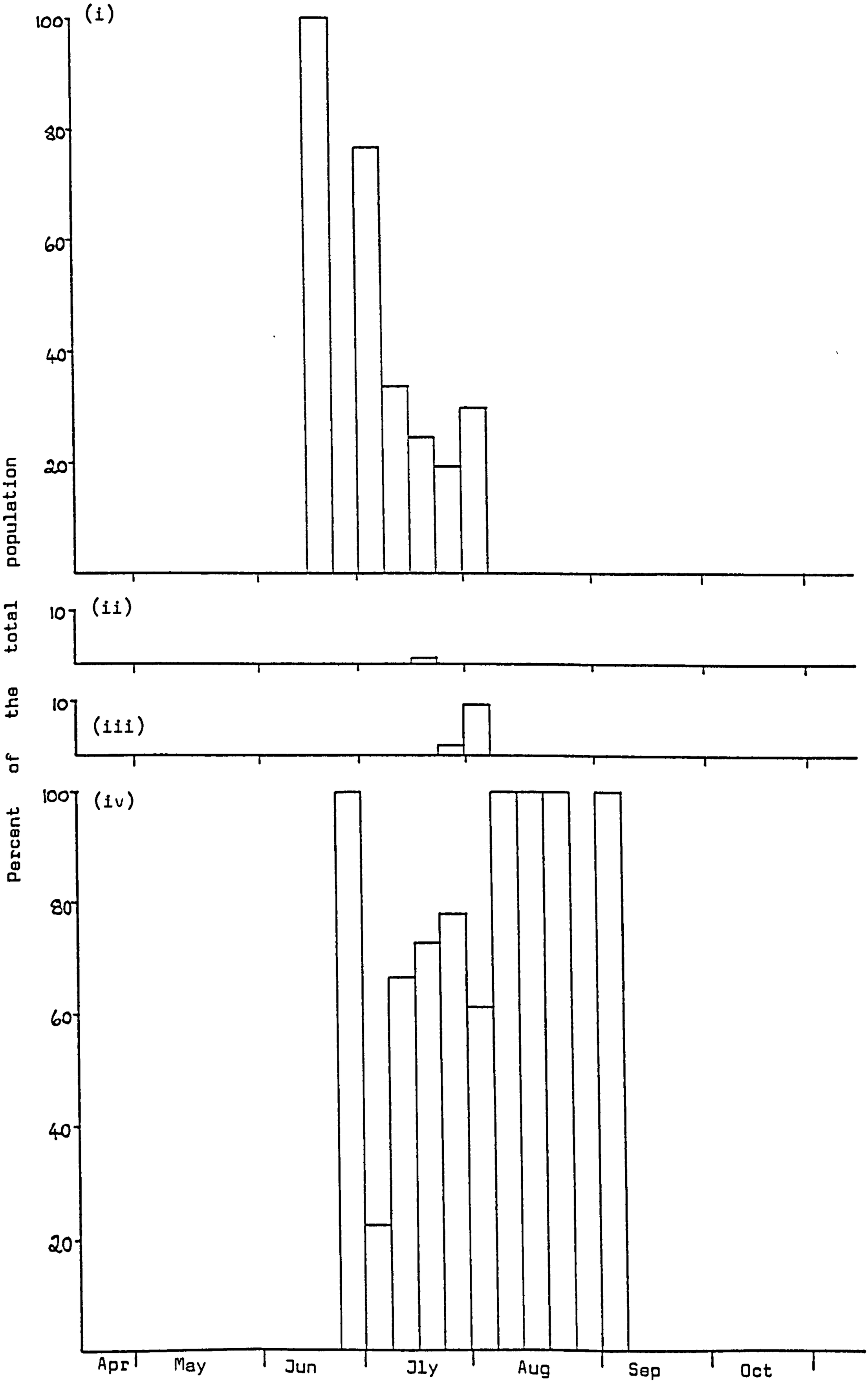
Section B, 1983

(i) Alate adults

(ii) Apterous adults

(iii) Fourth instars (presumptive apterae)

(iv) Nymphs


(i)
100
80
60
40
20
population
(ii)
10
total
(iii)
10
of the
(iv)
Percent
100
80
60
40
20
Apr
May
Jun
Jly
Aug
Sep
Oct

were found on either section.

(ii) Spatial distribution of aphids

All values of b were significantly different from unity (table 26) indicating that the aphids, when present, were aggregated. The values of Morisita's index (table 22) were high when the alates first appeared but fell as the numbers increased and more leaves were colonized.

(iii) Abundance of natural enemies

Adults of B.angulatus were recorded during August but no nymphs were found previously, suggesting that these had arrived on this alder from elsewhere. Occasional mummified carcasses were also found in samples.

2.5.9. WM110, 1984

(i) Abundance of aphids

Section 2 was pruned in late January. Sections 1 and 3 were pruned between July 12th and 19th and section 2 left uncut during the summer.

Aphid numbers appeared to be very low in the spring, a likely result of the small numbers of oviparae found the previous autumn. No fundatrices were found on any section and the first nymphs recorded appeared at the start of June. Numbers began to increase but the rise became more rapid when adults of the second generation appeared in late June. (figs.100-102). Sections 1 and 3 were pruned at the time when the populations were increasing. The pruning appeared to check the populations as the increase on these sections was considerably less than that on the uncut section 2. The population on each section peaked on August 2nd but numbers were much higher on section 2 than on 1 or 3. (table 23). Numbers declined sharply but reached lower levels on section 2 than on the other sections. The pattern of abundance on terminal and non terminal leaves was similar

Table 22 MORISITA'S INDEX OF DISPERSION - WM109, 1983

Date		SECTION A		SECTION B	
		Terminal leaves	Non-terminal leaves	Terminal leaves	Non-terminal leaves
April	25		0		
May	2		0		
June	13	0	0		
	20	20.0	100.0	0	0
	27	12.5	60.0	0	0
July	4	18.2	20.8	30.3	15.1
	11	9.6	5.7	6.8	5.1
	18	8.5	3.7	5.8	4.0
	25	6.4	10.5	12.2	4.0
Aug	1	9.4	3.1	5.7	5.5
	8		0		0
	15	0	0	0	0
	22	0	0	0	
	29				
Sept	5				0

Figure 100:

Aphid populations on WM 110, Section 1, 1984

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

Arrow represents date of pruning

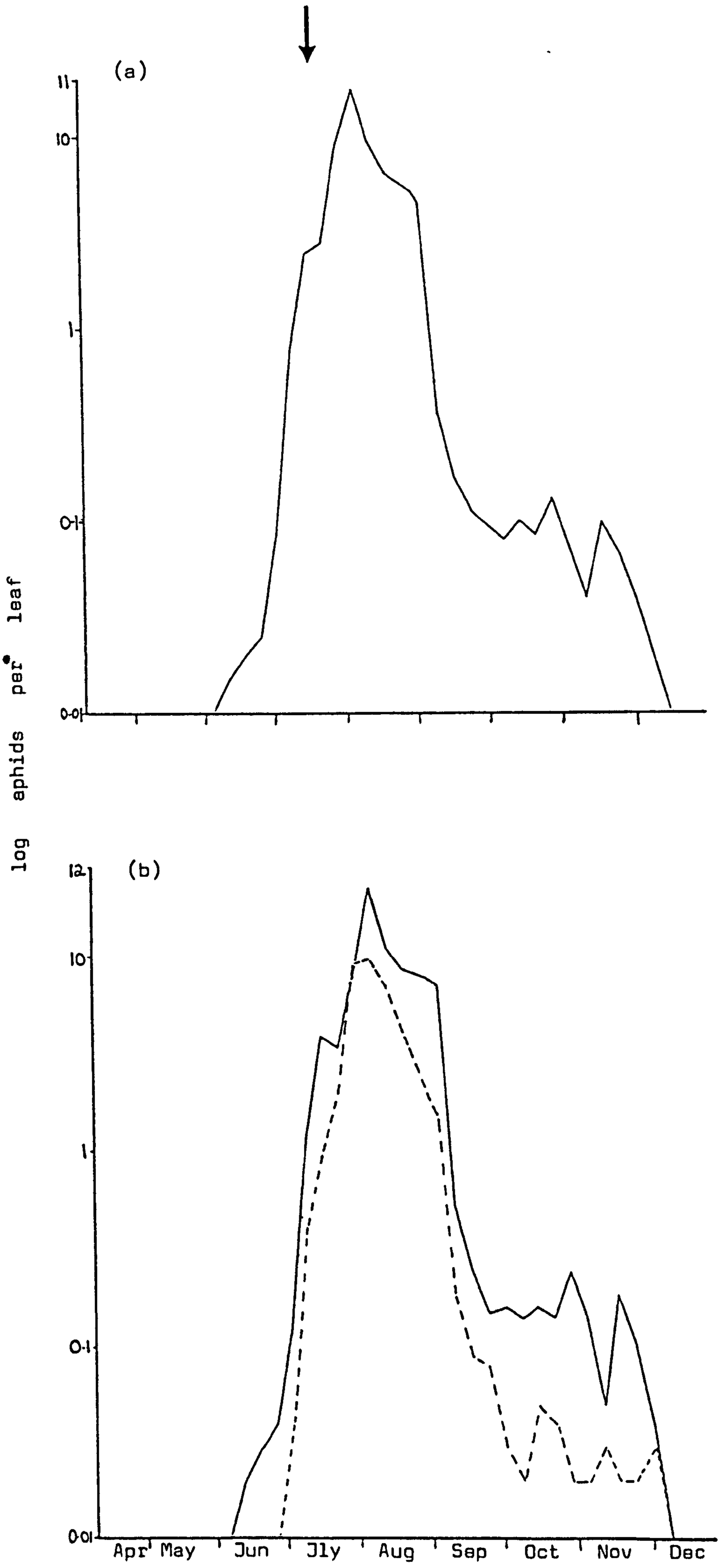

(a)
11
10
1
0·1
0·01
log apr hids per leaf
(b)
12
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov
Dec

Figure 101:

Aphid population on WM 110 section 2, 1984

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

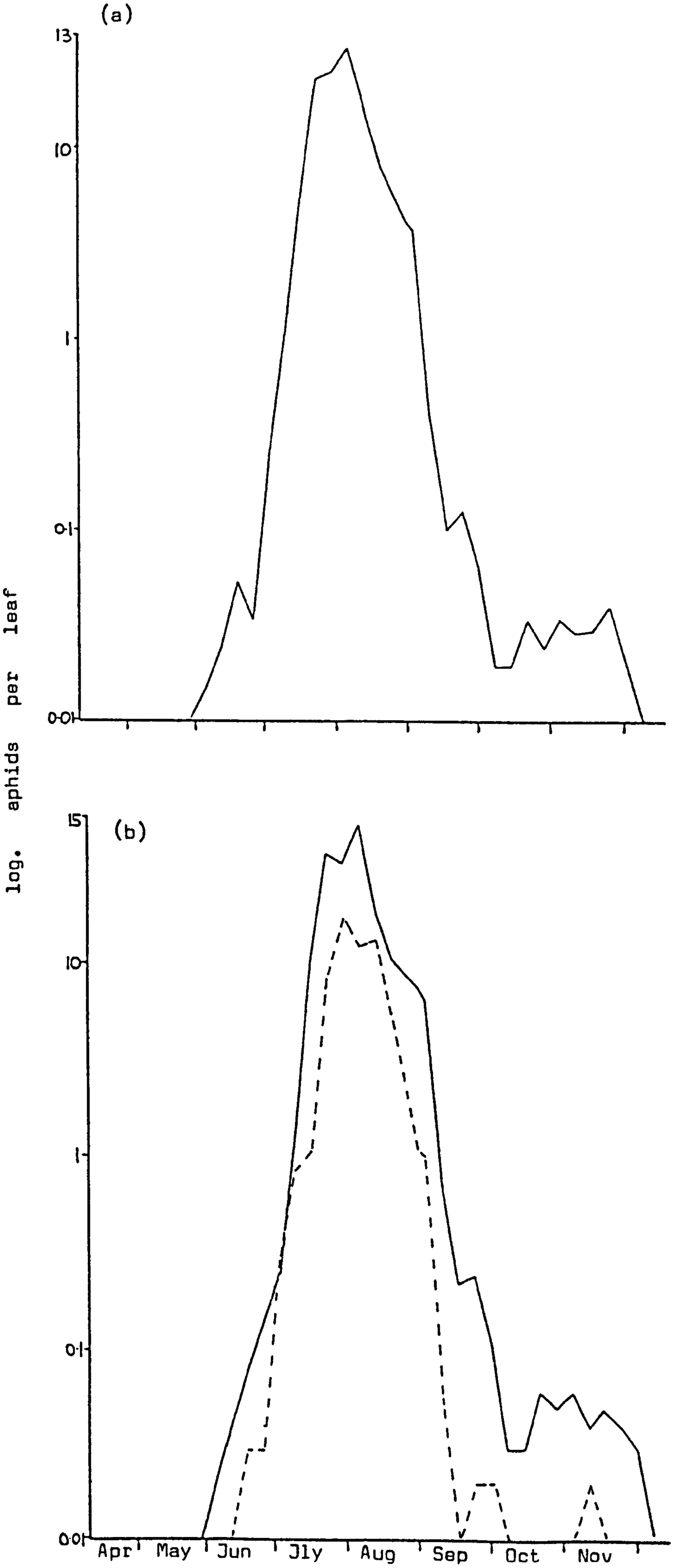

(a)
13
10
1
0·1
0·01
log. aphids per leaf
(b)
15
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 102:

Aphid populations on WM 110, section 3, 1984

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

Arrow represents date of pruning

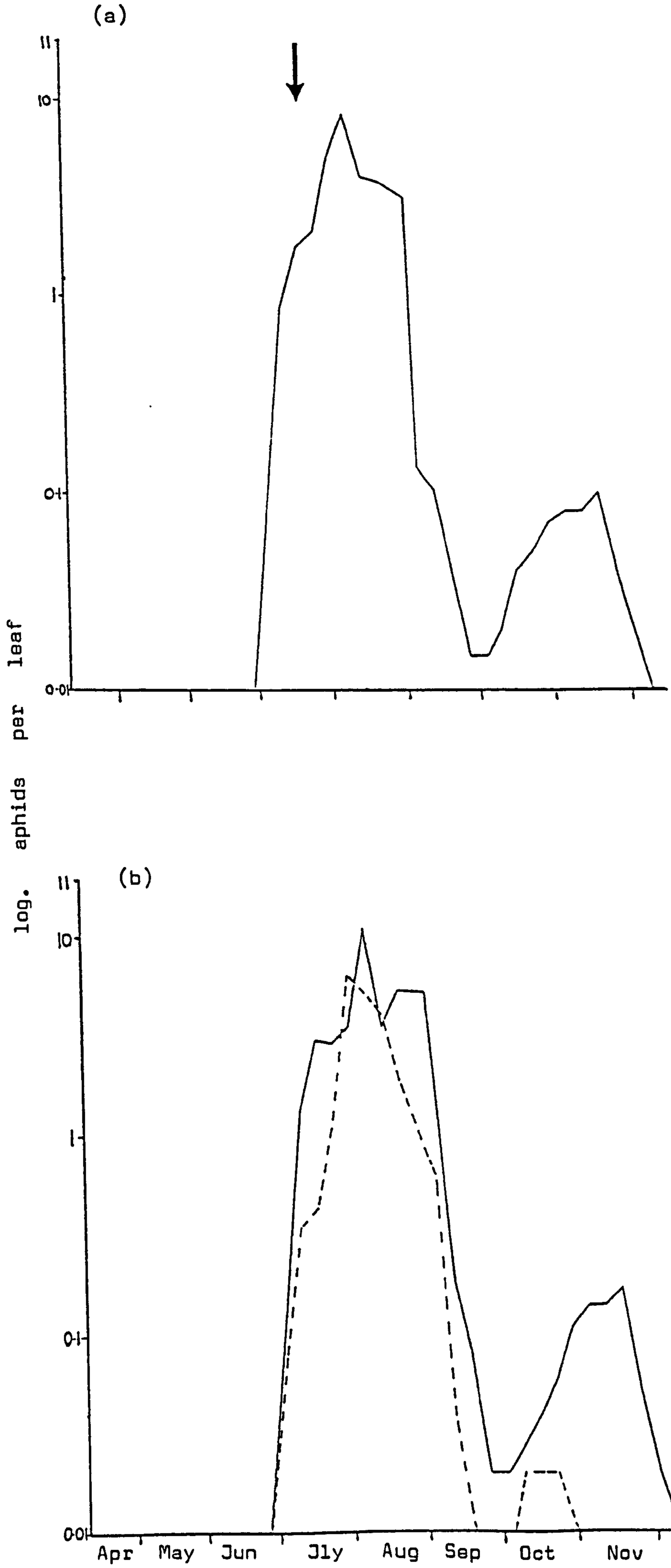

(a)
11
10
1
0·1
0·01
log. aphids per leaf
(b)
11
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov
Dec

Table 23 TOTAL NUMBER OF APHIDS IN LEAF SAMPLES - WM110, 1984

		SECTION 1			SECTION 2			SECTION 3		
Date		Aphids/ 100 Terminal leaves	Aphids/ 100 Non-terminal leaves	Aphids/ Whole sample	Aphids/ 100 Terminal leaves	Aphids/ 100 Non-terminal leaves	Aphids/ Whole sample	Aphids/ 100 Terminal leaves	Aphids/ 100 Non-terminal leaves	Aphids/ Whole sample
April	26	0	0	0	0	0	0	0	0	0
May	3	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0	0
	24	0	0	0	0	0	0	0	0	0
	31	0	0	0	0	1	1	0	0	0
June	7	0	1	1	0	3	3	0	0	0
	14	0	2	2	2	7	9	0	0	0
	21	0	3	3	2	3	5	0	0	0
	28	3	12	15	28	24	52	6	12	18
July	5	40	117	157	74	234	308	35	136	171
	12	95	393	488	106	1087	1193	44	307	351
	19	206	344	550	836	3878	4714	124	296	420
	26	927	854	1781	1716	2412	5128	650	362	1012
Aug	2	997	2448	3445	1229	5572	6801	525	1129	1654
	9	703	1129	1832	1386	1938	3324	419	365	784
	16	417	886	1303	549	1082	1631	196	547	743
	27	186	446	632	105	659	764	65	207	272
	30	158	938	1096	110	760	870	86	541	621
Sept	6	18	55	73	5	73	78	3	18	21
	13	8	24	32	0	21	21	0	6	6
	20	7	14	21	1	23	24	0	1	1
	27	2	15	17	1	10	11	0	1	1
Oct	5	1	13	14	0	2	2	2	4	6
	12	3	15	18	0	2	2	2	8	10
	18	2	13	15	0	5	5	0	14	14
	26	1	23	24	0	3	3	0	16	16
Nov	2	1	13	14	0	5	5	0	20	20
	9	2	4	6	1	3	4	0	13	13

on each section and mirrored that of the total population (figs.100-102).

Generally the population density was greatest on terminal leaves during the period of population increase (fig.103). After pruning this trend tended to be reversed on sections 1 and 3 but this reversal did not occur until later in the season on section 2. As with 1983, the redistribution of aphids over the leaves once the youngest ones were removed is a likely cause of this reversal.

Whilst the populations were increasing, instars I-III generally accounted for over 80% of the population (figs.104-106). This proportion remained high for the rest of the season, with alate adults comprising a third of the population in late August. Proportions of nymphs remained high until the end of the season with less fluctuation, a likely result of the higher numbers present than at the corresponding time in 1983. There were differences in the age structure of the populations on terminal and non-terminal leaves (appendix 2.9,2.10,2.11). Those on terminal leaves tended to contain higher proportions of fourth instars (potential alatae) and those on non terminals more winged adults. Alate adults were again recorded before fourth instars (potential alatae) were found. On this windbreak however alatae were first produced in the third generation in early July. Numbers rapidly increased and by late July the fourth instar was entirely potential alatae (fig.107). Alate adults were produced until the end of August, later than in 1983 (fig.90).

As previously stated, no examples of the first generation were found. The second generation was entirely apterous. Some alatae were produced in the third and fifth generations and the fourth, in early August, was entirely alate. The sixth generation during September contained no alate individuals. The offspring of these were the sexual forms of the seventh generation.

Figure 103:

Population density of P.alni on WM 110, 1984

(a) Section 1

(b) Section 2

(c) Section 3

- - - Terminal leaves

——— Non-terminal leaves

Arrows represent pruning

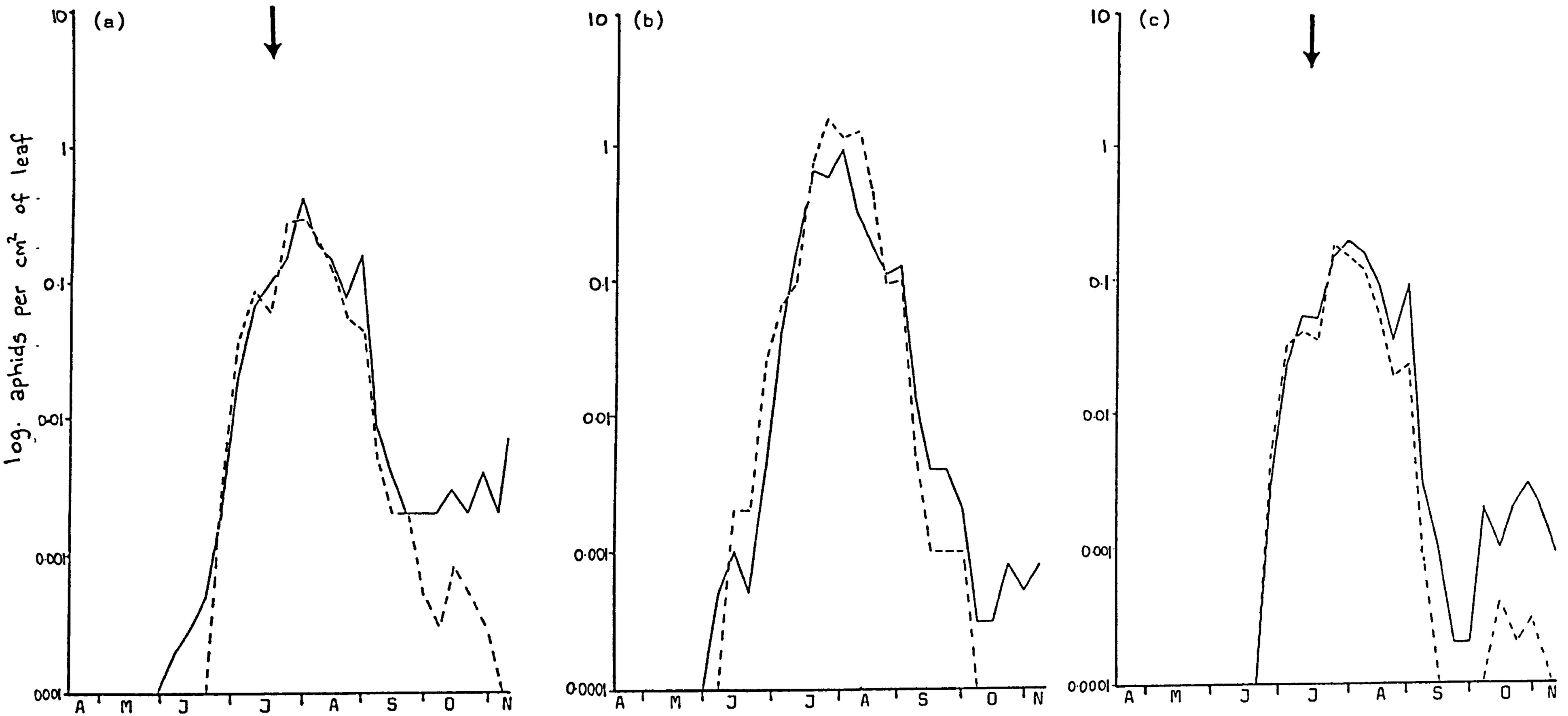

(a)
(b)
(c)
log. aphids per cm² of leaf
10
1
0·1
0·01
0·001
0·0001
A
M
J
J
A
S
O
N

Figure 104:

Age structure of the population on WM 110

Section 1, 1984

(i) Alate adults

(ii) Fourth instars (presumptive alatae)

(iii) Apterous adults

(iv) Fourth instars (presumptive apterae)

(v) Nymphs

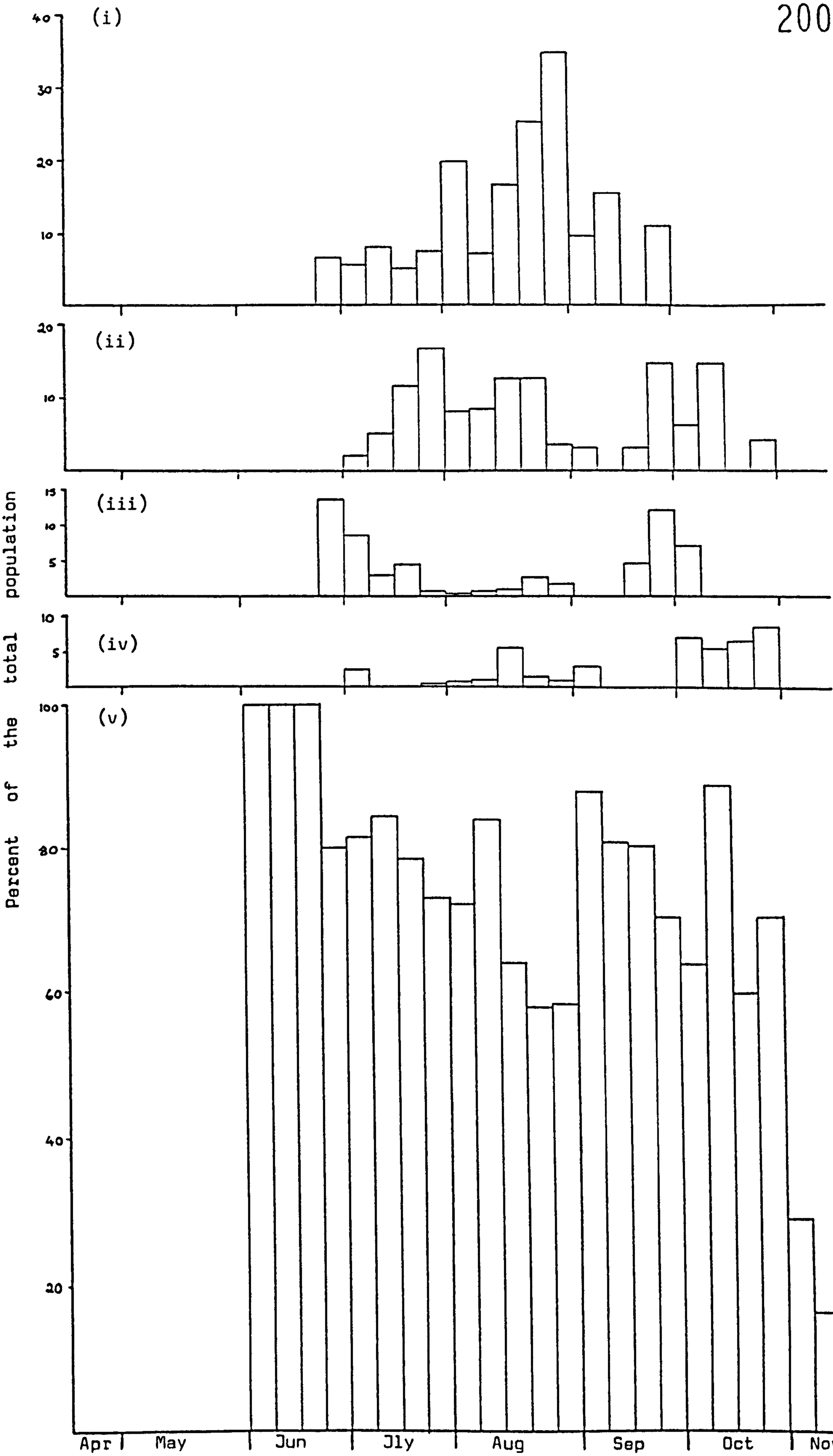

(i)
40
30
20
10
(ii)
20
10
(iii)
15
10
5
population
(iv)
10
5
total
(v)
100
80
60
40
20
Percent of the
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 105:

Age structure of the population on WM 110,

Section 2, 1984

For legend see figure 104

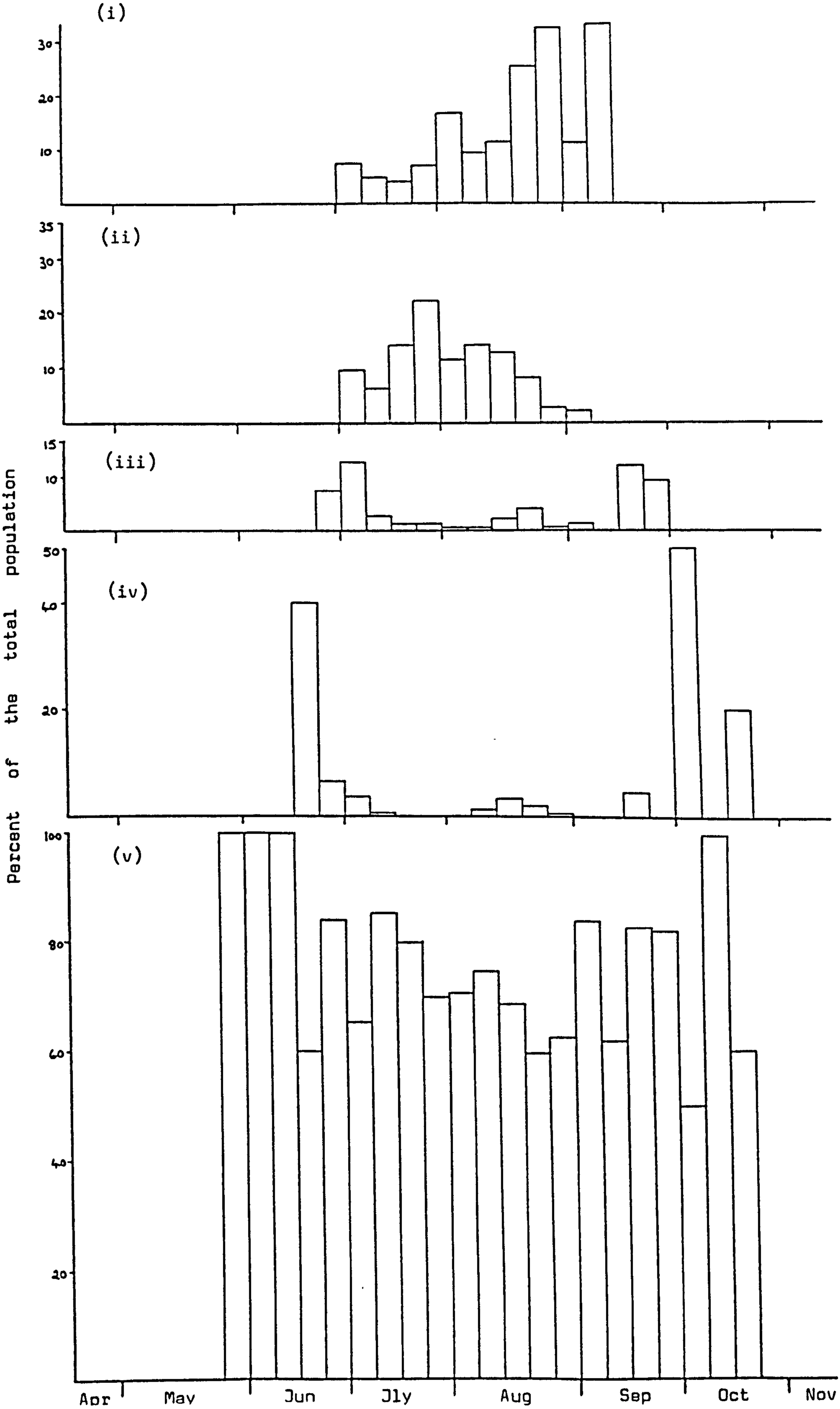
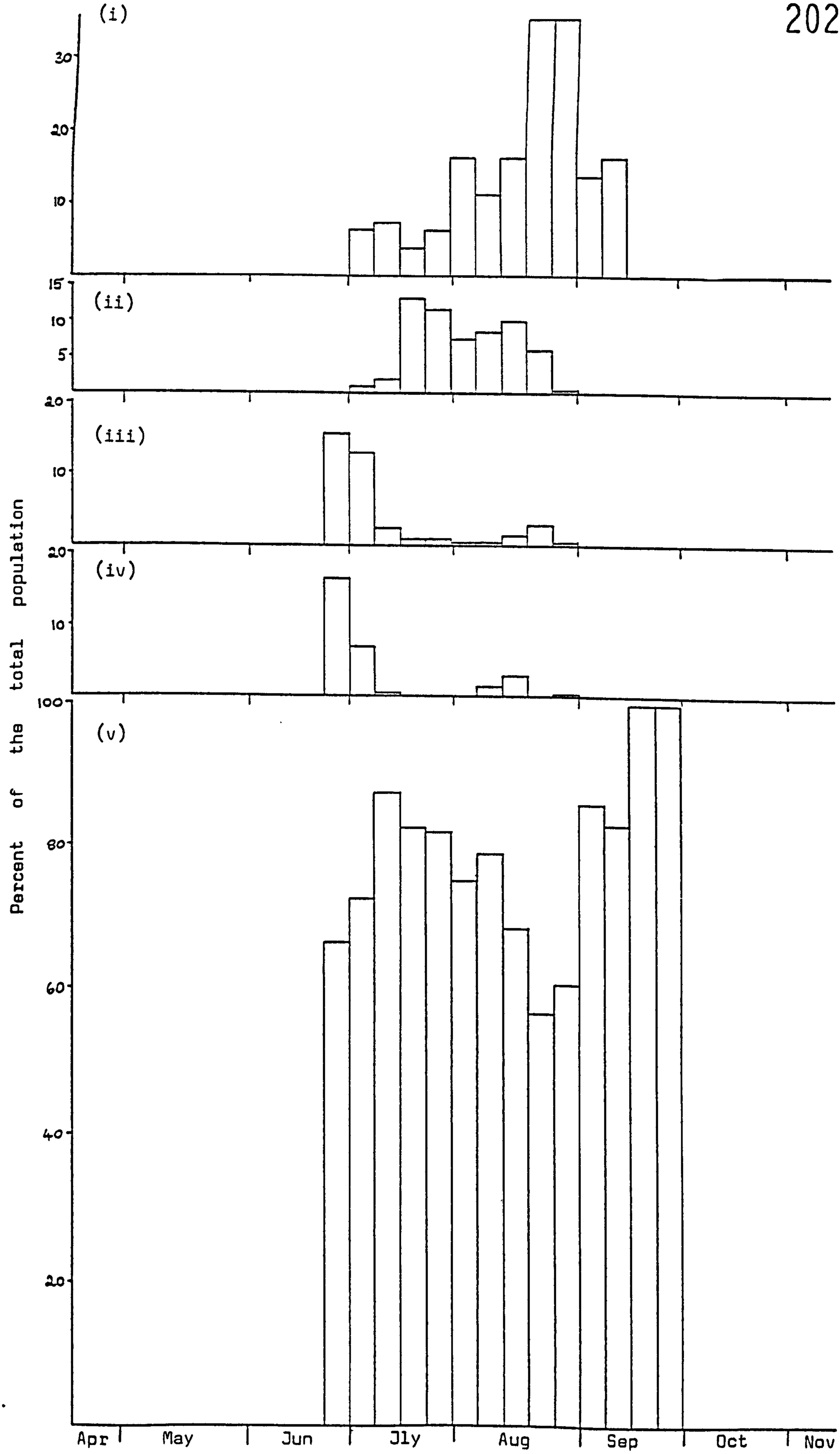

(i)
30
20
10
(ii)
35
30
20
10
(iii)
15
10
5
(iv)
50
40
30
20
10
(v)
100
80
60
40
20
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 106:

Age structure of the population on WM 110,

Section 3, 1984

For legend, see figure 104.


(i)
30
20
10
(ii)
15
10
5
(iii)
20
10
(iv)
20
10
(v)
100
80
60
40
20
Percent of the total population
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

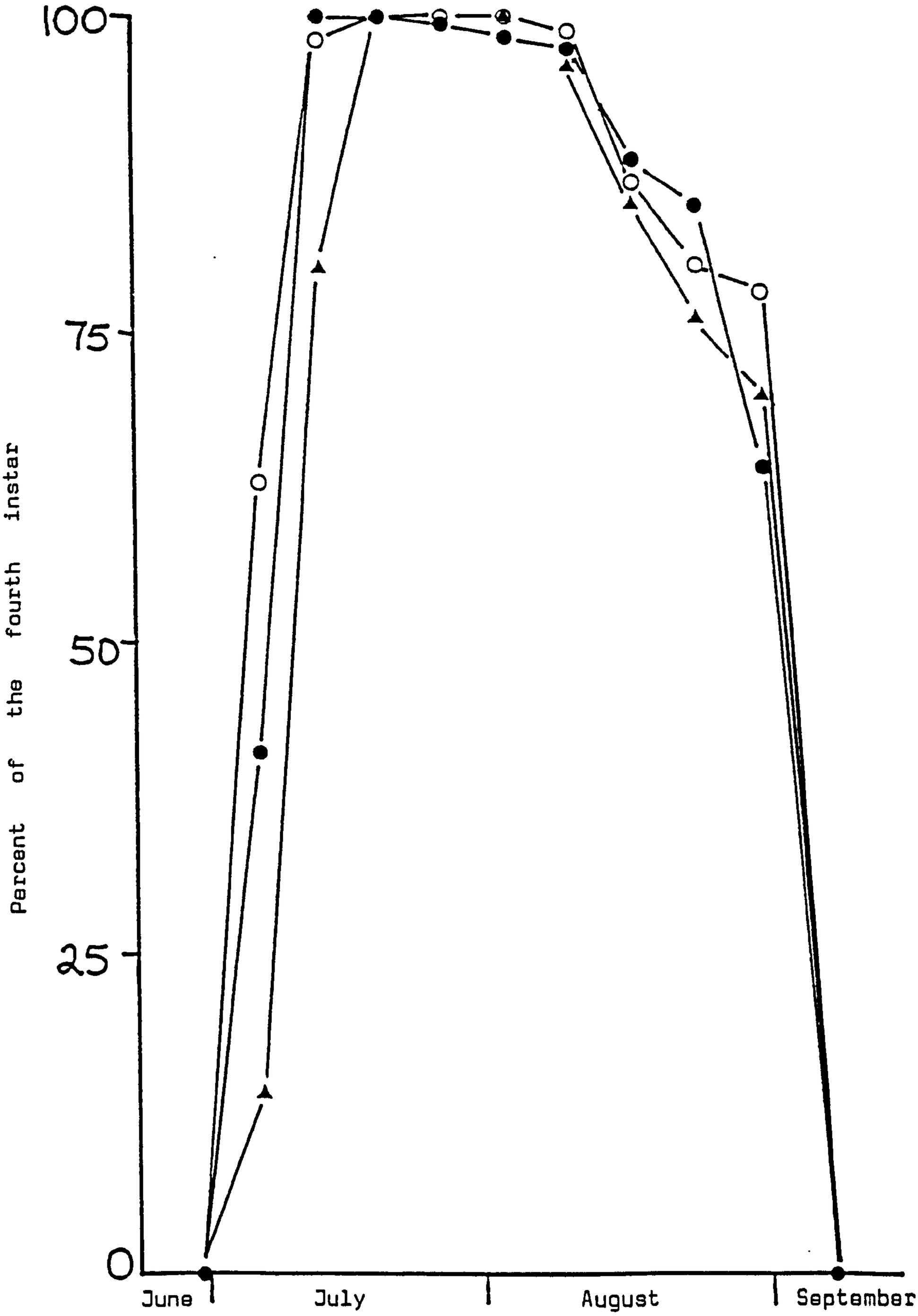


Figure 107: Proportion of presumptive alatae in the fourth instar, WM 110, 1984

●—● Section 1
○—○ Section 2
▲—▲ section 3

Males were recorded in late September and early October and oviparae from early October until leaf fall in late November (fig.108). A solitary ovipara was found on December 15th - the latest date ever recorded. Oviparae were more common on sections 1 and 3 than in 1983 (section 1, $d=3.03$, $p<0.01$; section 3, $d=2.85$, $p<0.01$) and similar on section 2 ($d=1.52$, $p>0.05$). The numbers of oviparae were similar on sections 1 and 3 and commoner on these sections compared to section 2 (fig.108) (sections 1 and 3, $d=0.23$, $p>0.05$; section 1 and 2, $d=2.36$, $p<0.05$; sections 2 and 3, $d=2.03$, $p<0.05$).

(ii) Spatial distribution of aphids

All values of b on terminal and non terminal leaves for each section were significantly different from unity (table 26), indicating that the aphids were aggregated over the season. The weekly values of Morisita's index (table 24) followed a very similar pattern to those described previously for LF125 and WM110 in 1982 and 1983. Aphids were not present for such a long period as in previous years but the index was high when aphids first appeared, falling as the population increased. The index increased with the late summer reproduction of the apterous generations and assumed zero indicating a regular distribution of aphids between the leaves.

(iii) Abundance of natural enemies

Predator numbers were similar on all sections (sections 1 and 2, $d=0.99$, d.f.=34, $p>0.05$; sections 1 and 3, $t=0.15$, d.f.=46, $p>0.05$; sections 2 and 3, $t = 0.78$, d.f.=46, $p>0.05$). The total numbers throughout the season are shown in fig.109. No coccinellid or anthocorid adults were found during May as in previous seasons. This may have been due to the virtual absence of aphids on the windbreak during the spring. Total numbers were thus low to begin with, only isolated specimens of O.marginalis being found on sections 1 and 2.

Pruning appeared to have little effect upon the numbers of predators. In this season, the pruning took place at the beginning of the egg hatching

Figure 108:

Abundance of sexuales, WM 110 1984

(a) Appearance of sexuales,section 1

(b) Abundance of oviparae, section 1

(c) Appearance of sexuales,section 2

(d) Abundance of oviparae, section 2

(e) Appearance of sexuales,section 3

(f) Abundance of oviparae, section 3

Males

Oviparae

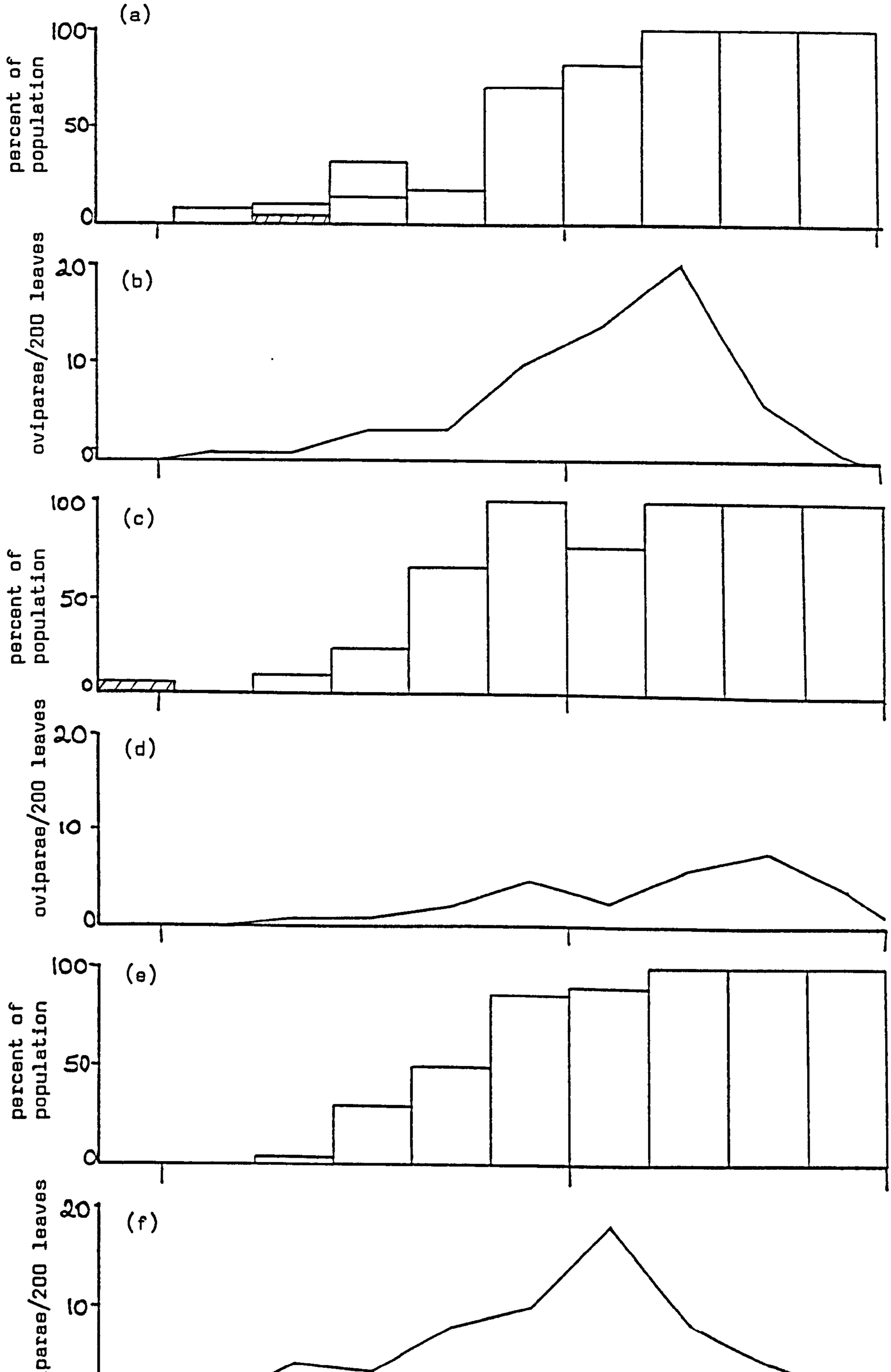

(a)
100
50
0
percent of population
(b)
20
10
0
ovipara e/200 leav
(c)
100
50
0
percent of population
(d)
20
10
0
ovipara e/200 leaves
(e)
100
50
0
percent of population
(f)
20
10
0
ovipara e/200 leaves
October
November

Table 24 MORISITA'S INDEX OF DISPERSION - WM110, 1984

Date		SECTION 1 Terminal leaves	SECTION 1 Non-terminal leaves	SECTION 2 Terminal leaves	SECTION 2 Non-terminal leaves	SECTION 3 Terminal leaves	SECTION 3 Non-terminal leaves
April	26						
May	3						
	10						
	17						
	24						
	31				0		
June	7		0		33.3		
	14		0	0	14.28		
	21		0	0	0		
	28	0	3.0	7.1	1.8	0	7.6
July	5	12.7	12.7	9.8	7.0	14.5	8.3
	12	8.6	4.4	10.1	4.6	8.6	2.2
	19	6.2	2.9	8.2	2.7	7.6	4.0
	26	3.5	4.7	2.9	2.1	2.9	2.8
Aug	2	2.3	1.9	2.2	1.7	2.9	2.0
	9	2.9	2.6	2.3	2.5	4.0	3.3
	16	4.4	2.1	2.7	1.9	5.0	3.3
	27	3.5	1.9	3.6	2.2	3.5	2.3
	30	4.7	2.1	3.9	2.2	6.4	2.3
Sept	6	1.3	4.0	10.0	3.9	0	9.2
	13	21.4	1.8		1.4		6.7
	20	9.5	3.3	0	4.4		0
	27	0	5.7	0	6.7		0
Oct	5	0	19.2		0		
	12	0	2.9		0		
	18	0	9.0		0		
	26	0	16.6		10.0		
Nov	2	0					
	9	0	0	0	0		

period for B.angulatus, shown by the appearance of nymphs and thus any nymphal loss due to pruning may have been obscured by the increase in numbers at this time. The ratio of predators to aphids fell as the aphid populations increased (fig.109). When the aphid numbers peaked this ratio was about 1 per 500 aphids, and rose to about 1 to every 6 aphids on each section at the end of the season. The greater number of predators on section 2 appears to have been largely caused by the number of larvae of S.ribesii, E.balteatus and M.luniger found. On sections 1 and 3 these accounted for 10 and 6% respectively of predator numbers, whereas on section 2 they represented 28% (fig.110). S.ribesii was the commonest accounting for 84% of larvae found. E.balteatus accounted for 14% and M.luniger 2%.

A.bipunctata was the only coccinellid recorded. A.nemorum and less commonly A.nemoralis represented the Anthocoridae. On each section, B.angulatus was most abundant, comprising 58% (section 1), 46% (section 2) and 55% (section 3) of total numbers. Nymphs appeared in mid July and adult females persisted until late September (fig.111). Larvae of C.carnea H.humulinus and A.aphidimyza were found occasionally. Parasitism by T.pallidus was first observed in mid July, later than in previous years and later than LF125 in 1984. This was a likely result of the lack of aphids during June. The percentage of adults parasitized on each section was similar with a rate of about 12% (fig.112). No examples of aphids killed by fungi were found.

2.5.10. WM109, 1984

(i) Abundance of aphids

Both sections were pruned between July 12th and 19th. No aphids were found on either section during April, May and June. Alate adults and young nymphs were first found in mid July and the populations then began to increase (figs.113,114). Aphids were much scarcer than in 1983 and the numbers declined rapidly from late August onwards. No aphids were

Figure 109:

Abundance of predators, WM 110, 1984

(a) Total numbers of predators,section 1

(b) Ratio of predators to aphids,section 1

(c) Total numbers of predators,section 2

(d) Ratio of predators to aphids,section 2

(e) Total numbers of predators,section 2

(f) Ratio of predators to aphids,section 3

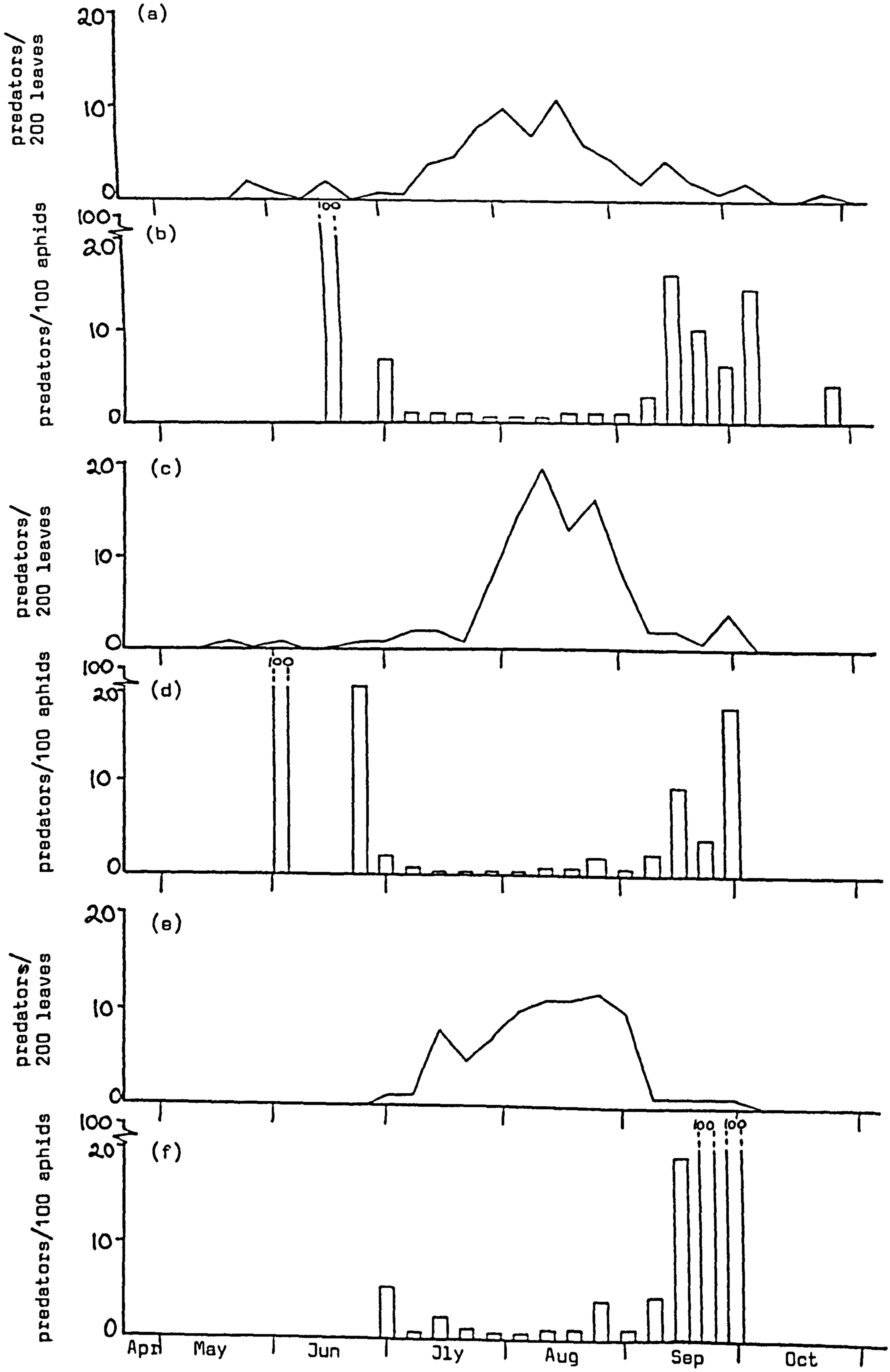

(a)
predators/
200 leaves
20
10
0
(b)
predators/100 aphids
100
20
10
0
(c)
predators/
200 leaves
20
10
0
(d)
predators/100 aphids
100
20
10
0
(e)
predators/
200 leaves
20
10
0
(f)
predators/100 aphids
100
20
10
0
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 110:

Relative abundance of predators, WM 110, 1984

(a) Section 1

(b) Section 2

(c) Section 3

(1) Coccinellidae

(2) Anthocoridae

(3) B.angulatus

(4) O.marginalis

(5) P.ambiguus

(6) Neuroptera

(7) Syrphidae

(8) Cecidomyiidae

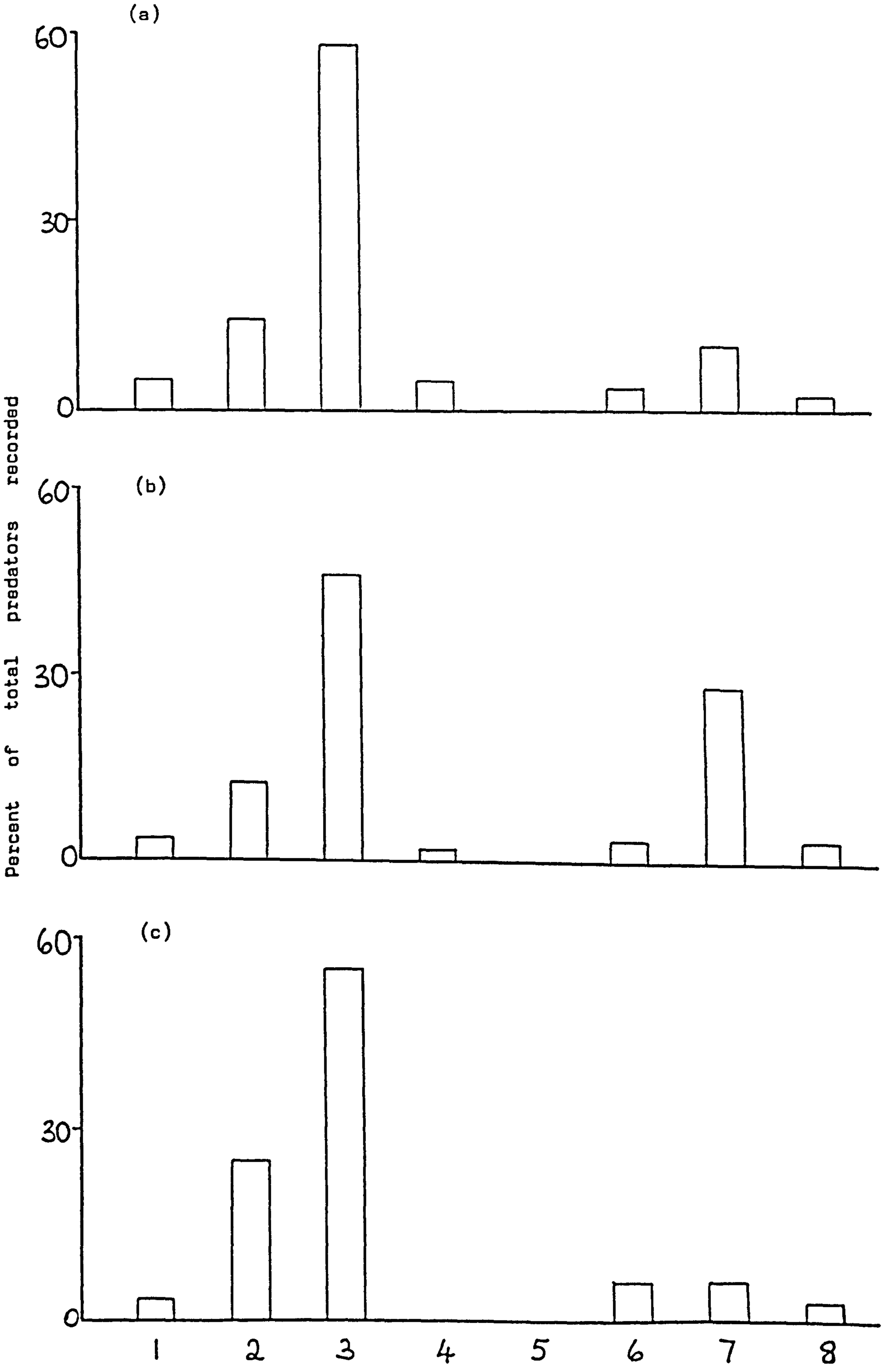

(a)
60
30
0
(b)
60
30
0
Percent of total predators recorded
(c)
60
30
0
1
2
3
4
5
6
7
8

Figure 111:

Numbers of B.angulatus on WM110, 1984

(a) Section 1

(b) Section 2

(c) Section 3

Nymphs

Males

Females

Figure 112:

Parasitism in populations of P.alni,

WM 110, 1984

(a) Section 1

(b) Section 2

(c) Section 3

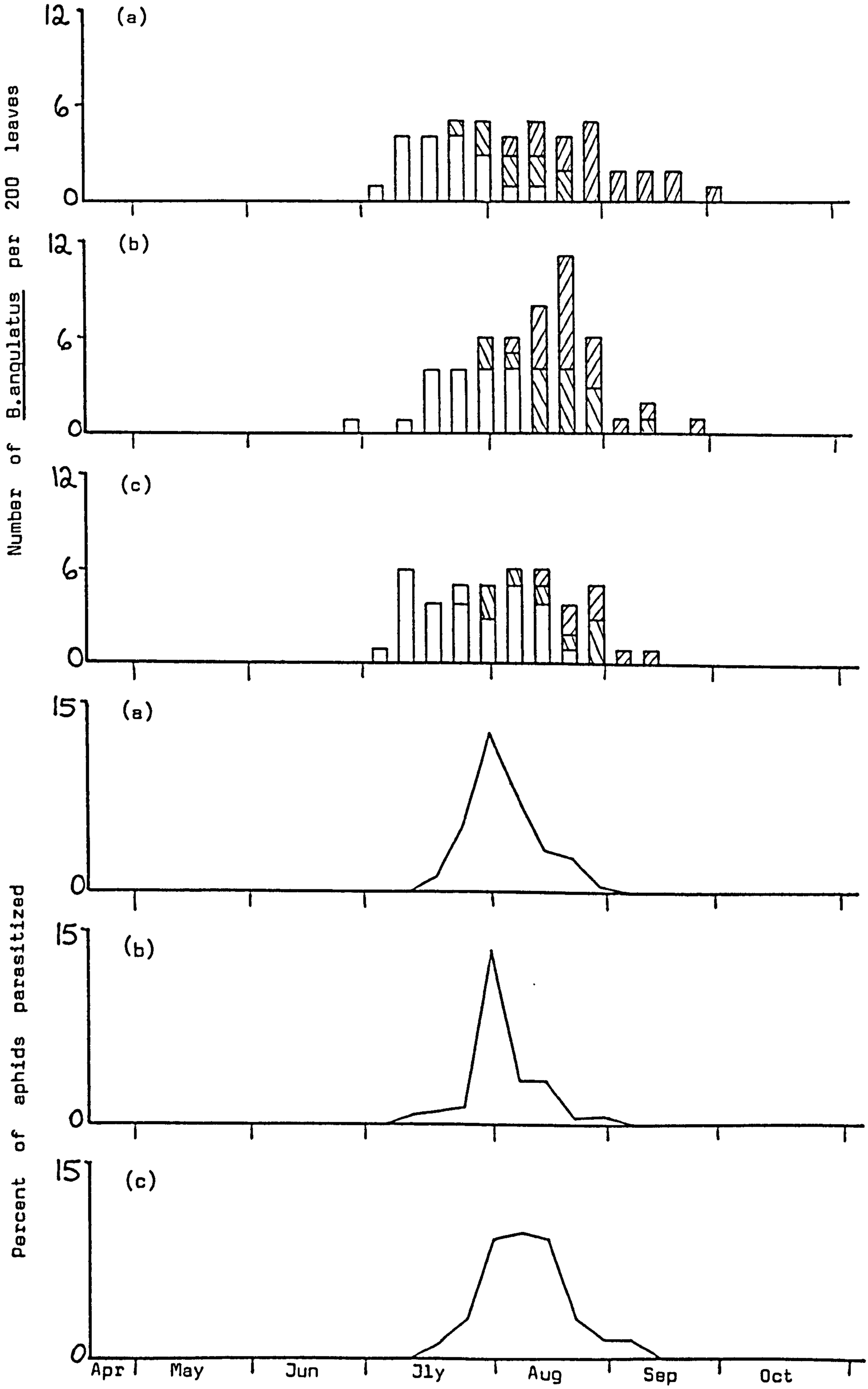

Number of B.angulatus per 200 leaves
(a)
12
6
0
(b)
12
6
0
(c)
12
6
0
Percent of aphids parasitized
(a)
15
0
(b)
15
0
(c)
15
0
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 113:

Aphid populations on WM 109,Section A,1984

(a) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

(b) 200 leaf sample

Arrow represents pruning

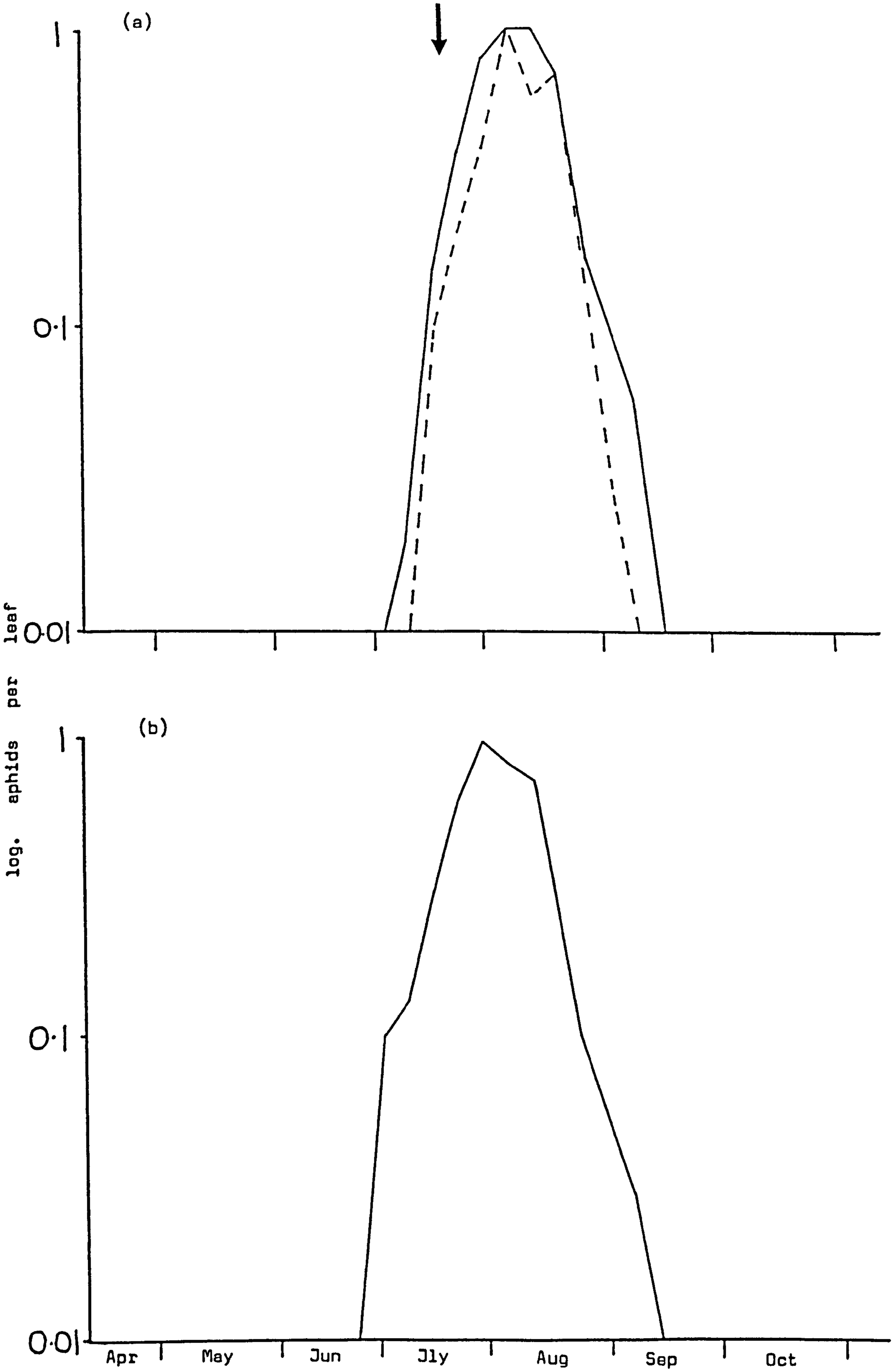

(a)
1
0·1
0·01
log. aphids per leaf
(b)
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct

Figure 114:

Aphid populations on WM 109,section B, 1984

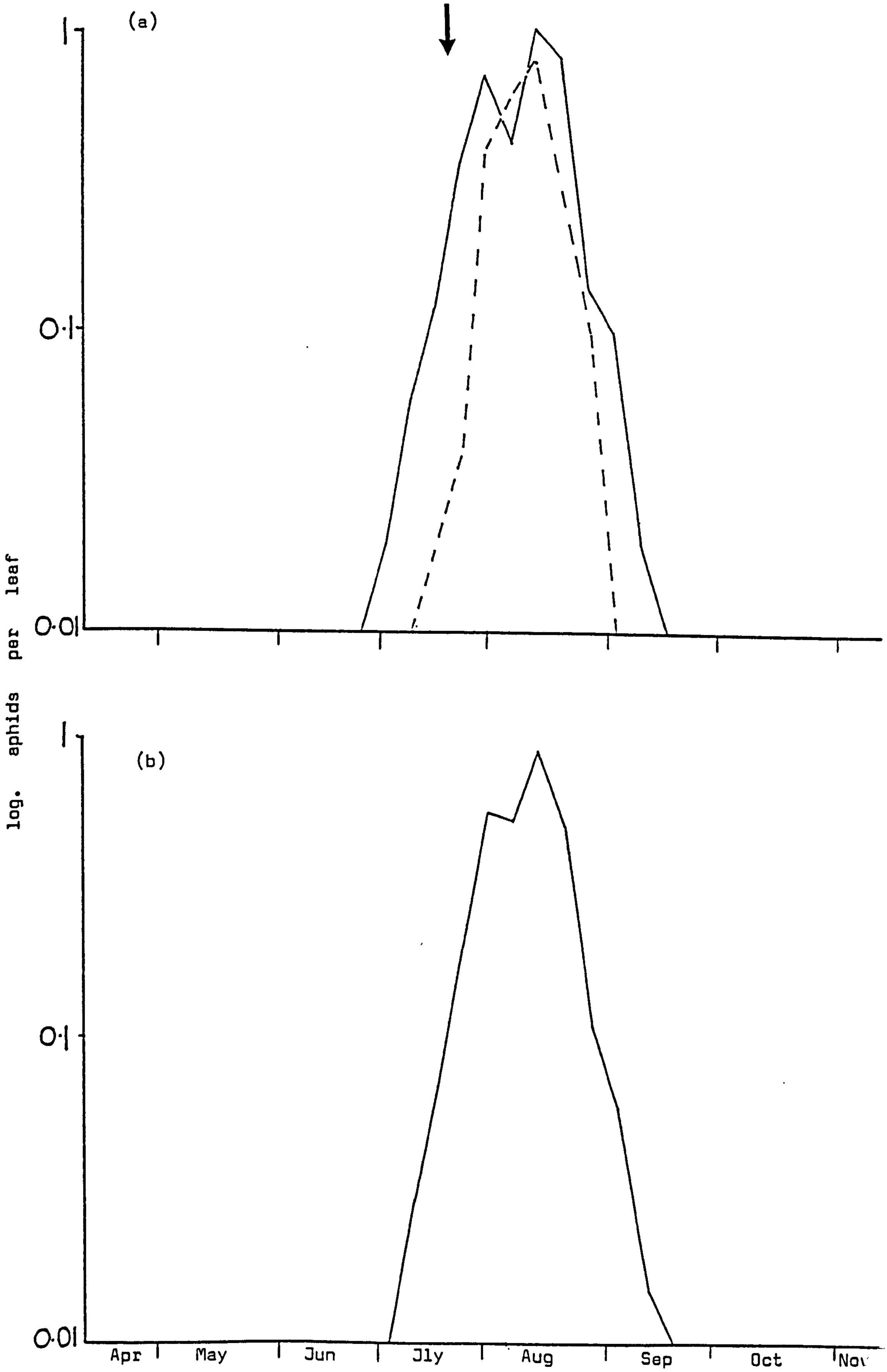
(a) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

(b) 200 leaf sample

Arrow represents pruning


(a)
1
0·1
0·01
per leaf
(b)
log. aphids
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

found after early September. Populations consisted almost entirely of alate adults and young nymphs. The proportions of each fluctuated, but in general, instars I-III comprised 60-80% of the population. Some apterous fourth instars were found but no apterous adults recorded.

(ii) Spatial distribution of aphids

All values of b were significantly different from unity (table 26) indicating that during the period of abundance the aphids were aggregated. The values of Morisita's index (table 25) were high when aphids first appeared and fell as more leaves were colonized. In general values were higher than on WM110. A likely cause is that the distribution on WM109 was very 'patchy' caused by alates arriving and reproducing. Thus although few leaves were colonized, those that were had groups of aphids upon them.

(iii) Abundance of natural enemies

Isolated adults of B.angulatus were found in late August. No nymphs were found previously and the arrival on WM109 coincided with the decline in numbers of these bugs on WM110, suggesting a migration from one windbreak to the other. A few mummified carcasses were found on each section in late August.

2.5.11. The vertical distribution of aphids, 1983

(i) Abundance of aphids

A scaffold tower 8m high was erected in early 1983 adjacent to windbreak WM110 (fig.1). This enabled the leaves of four trees to be sampled. Tractor pruning of the trees enclosed by the tower was not possible. Thus the tower was erected in section 2 and the branches pruned in winter with hand shears. Leaf samples were taken at 3.5m and 7.5m, the middle and top of the windbreak.

Table 25 MORISITA'S INDEX OF DISPERSION - WM109, 1984

Date		SECTION A		SECTION B	
		Terminal leaves	Non-terminal leaves	Terminal leaves	Non-terminal leaves
June	7				
	14		100.0		60.0
	21		40.0		19.8
	28	16.7	15.2		2.1
July	5	10.8	3.7	20.0	7.4
	12		5.2	3.1	4.1
	19		4.8		5.5
	26	0	3.0		3.4
Aug	2	0	2.6	2.0	6.1
	9	0	0		10.1
	16		0		0
	27		0		0
	30		0		
Sept	6		0		10.1
	13		0		

Table 26 REGRESSION PARAMETERS OF LOG S^2 ON LOG $\bar{X}$ - EAST MALLING 1982,83 & 84

Sample	Date	Leaves	b	St.Error	a
WM110(1+2)	1982	T	1.47	0.040	6.22
WM110(1+2)	1982	NT	1.43	0.058	5.27
WM110 3	1982	T	1.49	0.043	6.58
WM110 3	1982	NT	1.38	0.078	4.69
WM110 1	1983	T	1.46	0.046	8.55
WM110 1	1983	NT	1.50	0.038	8.59
WM110 2	1983	T	1.49	0.051	9.44
WM110 2	1983	NT	1.53	0.03	8.33
WM110 3	1983	T	1.55	0.06	8.41
WM110 3	1983	NT	1.50	0.058	9.32
WM110 1	1984	T	1.46	0.031	6.24
WM110 1	1984	NT	1.47	0.046	5.09
WM110 2	1984	T	1.47	0.042	6.84
WM110 2	1984	NT	1.53	0.049	5.22
WM110 3	1984	T	1.53	0.059	5.81
WM110 3	1984	NT	1.38	0.041	4.89
WM109 A	1982	T	1.10 *	0.039	1.51
WM109 A	1982	NT	1.25 **	0.089	2.98
WM109 B	1982	T	1.42	0.097	5.19
WM109 B	1982	NT	1.45	0.129	4.81
WM109 A	1983	T	1.45	0.027	6.87
WM109 A	1983	NT	1.46	0.066	7.60
WM109 B	1983	T	1.33	0.064	4.72
WM109 B	1983	NT	1.35	0.023	4.53
WM109 A	1984	T	1.48	0.069	4.71
WM109 A	1984	NT	1.49	0.082	5.11
WM109 B	1984	T	1.37	0.046	4.32
WM109 B	1984	NT	1.39	0.051	4.46
LF125(1+2)	1982	T	1.48	0.089	7.23
LF125(1+2)	1982	NT	1.49	0.073	5.33
LF125 1	1983	T	1.51	0.041	7.85
LF125 1	1983	NT	1.56	0.035	6.70
LF125 2	1983	T	1.51	0.029	7.85
LF125 2	1983	NT	1.54	0.108	8.86
LF125 1	1984	T	1.54	0.078	8.64
LF125 1	1984	NT	1.55	0.053	9.24
LF125 2	1984	T	1.49	0.044	7.36
LF125 2	1984	NT	1.60	0.054	8.71

Significance levels * p 0.05
** p 0.01

All values of b significantly different from 1 at $p < 0.001$ except where indicated

Aphids appeared during May at both heights and original numbers of fundatrices were similar at each height ($d=0.64$, $p>0.05$) and to those of the main sampling programme (3.5m, $d=0.31$, $p>0.05$; 7.5m, $d=0.34$, $p>0.05$). The total numbers increased and the populations attained their peaks on July 21st, the same date as for the whole section (figs.115a,116a). The maximum attained at 3.5m was similar to that of the whole section ($d=0.86$, $p>0.05$) but at 7.5m, numbers were lower ($d=2.04$, $p<0.05$) (table 27). The populations declined sharply to low, but similar levels in autumn. The pattern of abundance on terminal and non terminal leaves was similar to the total populations with more aphids present on the non-terminal leaves (figs.115b,116b). As with the whole section however, the density of aphids was greater for most of the season on the terminal leaves than on the non-terminals.

Throughout the period of population increase, instars I-III accounted for 70-90% of the numbers at each height. The form of the generations was the same as that on the whole section; the first two generations were apterous, the third and fourth alate and the fifth and sixth apterous. The sexual forms comprised the seventh, last generation. The age structure of the populations was different on the terminal and non terminal leaves (appendix 2.12,2.13). During the period of rapid population increase and decline, the numbers on terminal leaves contained a higher proportion of fourth instars (potential alatae) and a lower proportion of alate adults. There also tended to be higher proportions of nymphs, fourths (potential apterae) and apterous adults on terminal leaves.

Alate adults were first produced in mid June and at the time of the population peak on July 21st the fourth instar was entirely potential alatae (fig.117). Alatae were produced until early August. Proportions were similar at each height and to those of the whole section (fig.90). Males and oviparae were recorded during October. Ovipara numbers were low

Figure 115:

Aphid populations at 3.5 m on WM110,

section 2, 1983

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

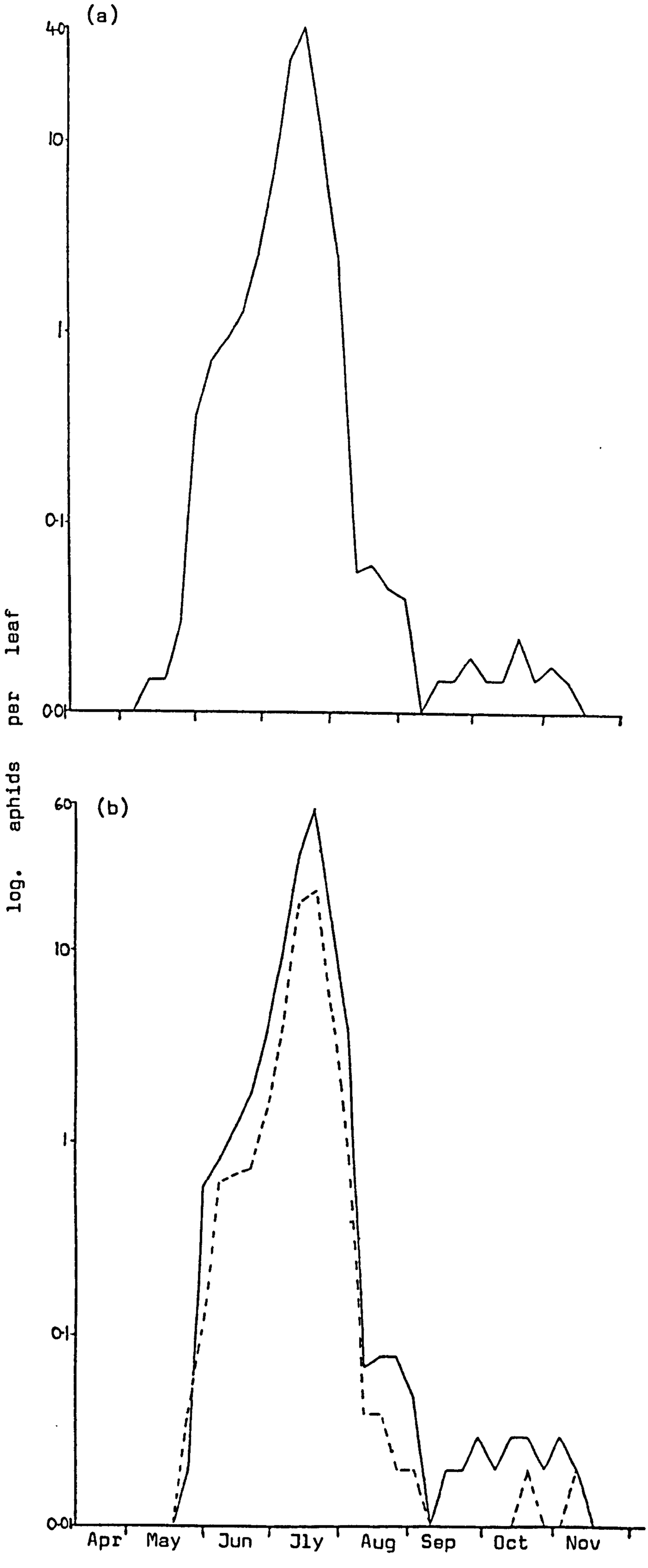

(a)
40
10
1
0·1
0·01
log. aphids per leaf
(b)
60
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 116:

Aphid populations at 7.5 m on WM 110,

Section 2, 1983

(a) 100 leaf sample

(b) 200 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

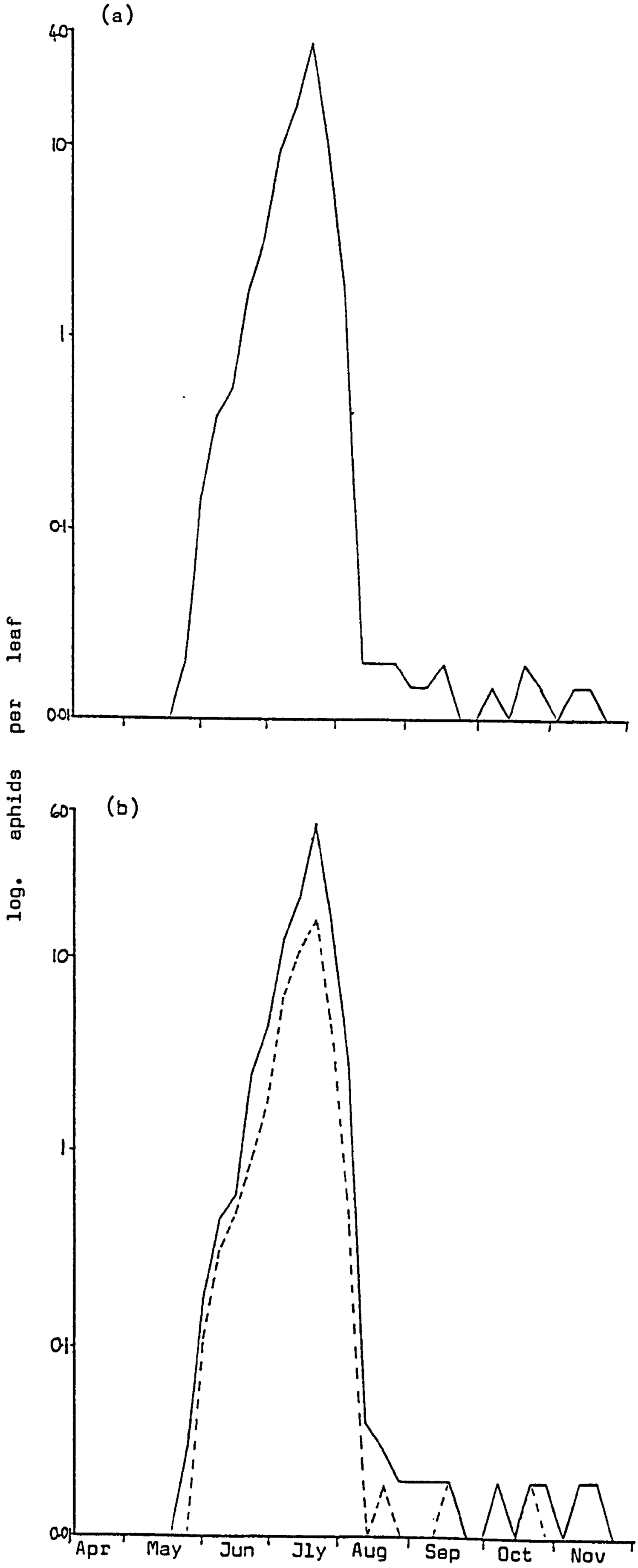

(a)
40
10
1
0·1
0·01
per leaf
log. aphids
(b)
60
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Table 27 TOTAL NUMBERS OF APHIDS IN SAMPLES - VERTICAL DISTRIBUTION, EAST MALLING 1983

		3.5 m			7.5 m		
		Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample	Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample
April	28	0	0	0	0	0	0
May	5	0	0	0	0	0	0
	12	1	0	1	0	0	0
	19	1	0	1	0	0	0
	26	4	2	6	1	3	4
June	2	12	59	71	11	18	29
	9	62	82	144	31	47	78
	16	69	119	188	48	60	108
	23	74	185	259	91	260	351
	30	147	378	525	187	458	645
July	7	409	927	1336	671	1271	1942
	14	1883	3385	5268	1091	2077	3168
	21	2010	5832	7842	1675	5214	6889
	28	496	1502	1998	407	1567	1974
Aug	4	97	404	501	47	294	341
	11	4	7	11	0	4	4
	18	4	8	12	1	3	4
	25	1	8	9	0	2	2
Sept	1	1	5	6	0	1	1
	8	0	0	0	0	1	1
	15	0	1	1	1	1	2
	22	0	1	1	0	0	0
	29	0	2	2	0	0	0
Oct	6	0	1	1	0	1	1
	13	0	2	2	0	0	0
	20	1	2	3	1	1	2
	27	0	1	1	0	1	1
Nov	3	0	2	2	0	0	0
	10	1	1	2	0	1	1
	17	0	0	0	0	1	1
	24	0	1	1	0	0	0

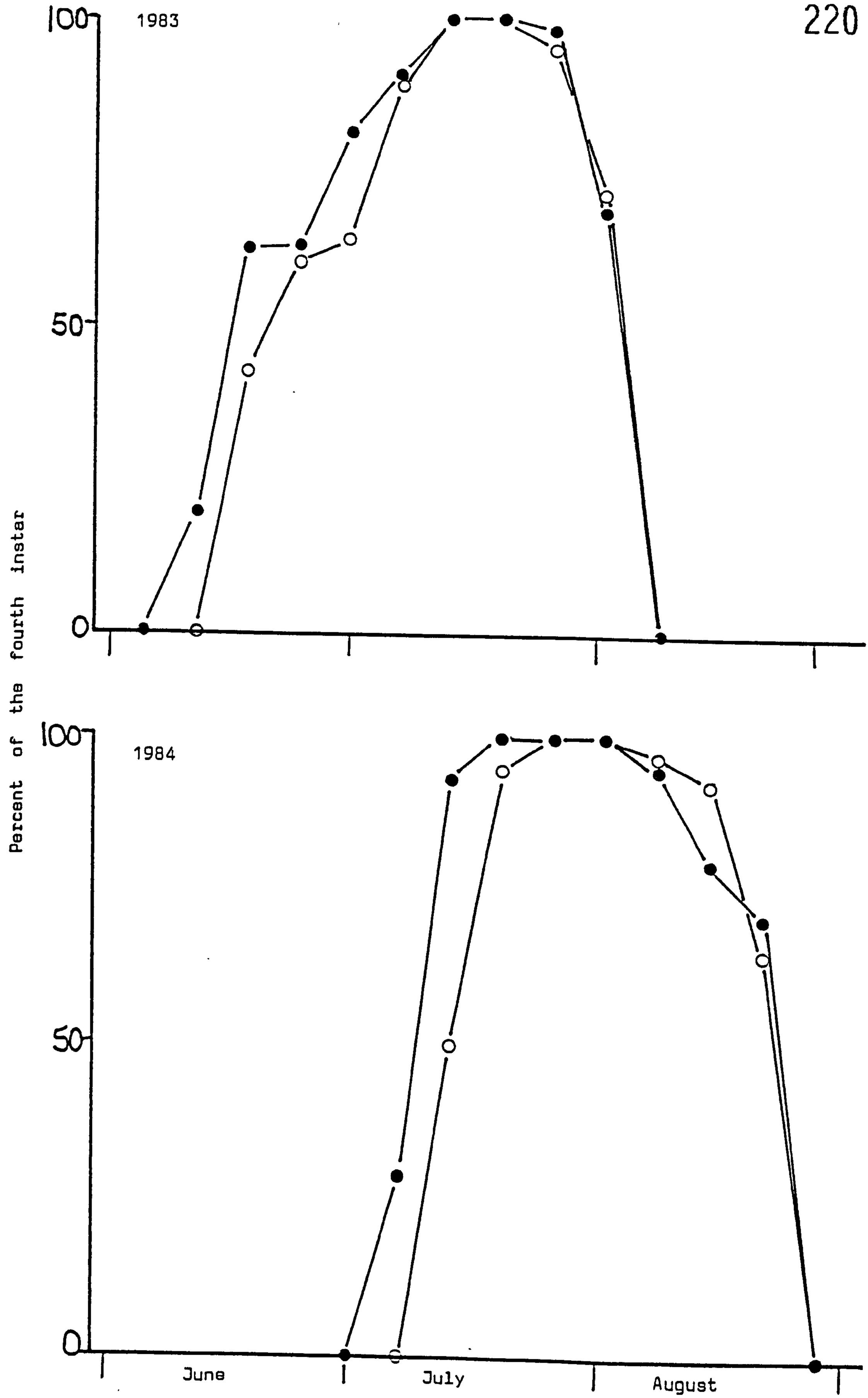
Figure 117:

Proportion of presumptive alatae in the

fourth instar WM 110 section 2, 1983 & 1984.

●—● 3.5 m

○—○ 7.5 m


1983
100
50
0
1984
100
50
0
Percent of the fourth instar
June
July
August

but there were no differences between the numbers at each height ($t=1.82, d.f.=14, p>0.05$) or between 3.5m and the whole section ($t=0.55, d.f.=14, p>0.05$). Oviparae were less common at 7.5m than on the whole section ($t=2.49, d.f.=14, p<0.05$).

(ii) Spatial distribution of aphids

All values of b were significantly different from unity (table 28) indicating that the aphids were aggregated over the whole season. The values of Morisita's index (table 29) showed the familiar trend of high values at the beginning and end of the season, with a fall as the aphid population increased with more leaves being colonized.

(iii) Abundance of natural enemies

Predators were similar in abundance at each height ($t=1.04, d.f.=52, p>0.05$) and to those on the whole section (3.5m, $t=0.70, d.f.=52, p>0.05$; 7.5m, $t=1.80$, $d.f.=52, p>0.05$). Total numbers are shown in fig.118a,b. The ratio of predators to aphids was low at 1 per 1000 during the period of increase in aphid abundance. When the aphids disappeared this rose to 1 per 2 aphids at 3.5m but due to the scarcity of predators during August at 7.5m to only 1 per 100 (fig.118b,d,).

Adults of A.nemorum and larvae of C.carnea were found at both heights and adults of A.bipunctata at 3.5m. As on the whole section (fig.93) larvae of S.ribesii and E.balteatus were the second commonest predators and both were found at each height. The commonest predator was again B.angulatus accounting for 72% of numbers at 3.5m and 67% at 7.5m.(fig.119). Nymphs appeared in late June and adults from late July onwards; females persisting until mid September (fig.120). Parasitism by T.pallidus was first observed in late June and rose to 8.2% by July 21st at 3.5m and to 6.8% on the same date at 7.5m. Neither of these values were significantly different from the rate of 11.1% observed on the whole

Table 28 REGRESSION PARAMETERS OF LOG S^2 ON LOG $\bar{X}$ AT 3.5M & 7.5M EAST MALLING, 1983 and 1984

1983

Height	Leaves	b	Standard error	a
3.5m	T	1.46	0.041	8.66
3.5m	NT	1.52	0.059	8.22
7.5m	T	1.44	0.048	7.21
7.5m	NT	1.48	0.061	7.44

1984

Height	Leaves	b	Standard error	a
3.5m	T	1.49	0.055	8.11
3.5m	NT	1.52	0.051	8.10
7.5m	T	1.50	0.062	7.49
7.5m	NT	1.54	0.049	8.41

All values of b significantly different from 1 at $p < 0.001$

Table 29 MORISITA'S INDEX OF DISPERSION AT 3.5M & 7.5M. 1983

Date		3·5m		7·5m	
		Terminal leaves	Non-terminal leaves	Terminal leaves	Non-terminal leaves
April	28				
May	5				
	12	0			
	19	0			
	26	0	0	0	0
June	2	14.1	28.2	33.3	41.0
	9	12.8	16.1	20.2	28.3
	16	9.4	10.1	15.4	16.1
	23	6.1	10.6	12.4	10.1
	30	10.2	12.1	8.3	3.8
July	7	11.1	15.1	6.4	4.2
	14	5.6	6.3	4.1	2.6
	21	2.8	3.1	3.0	2.4
	28	4.1	3.2	2.1	2.7
Aug	4	5.1	4.1	8.6	4.1
	11	0	21.0		20.0
	18	0	40.0	0	30.0
	25	0	18.2		0
Sept	1	0	0		0
	8				0
	15		0	0	0
	22		0		
	29		0		
Oct	6		0		0
	13		0		
	20	0	0	0	0
	27		0		0
Nov	3		0		
	10	0	0		0
	17				0
	24		0		

Figure 118:

Abundance of predators, WM 110,

Section 2, 1983

(a) Total numbers of predators, 3.5 m

(b) Ratio of predators to aphids, 3.5 m

(c) Total numbers of predators, 7.5 m

(d) Ratio of predators to aphids, 7.5 m

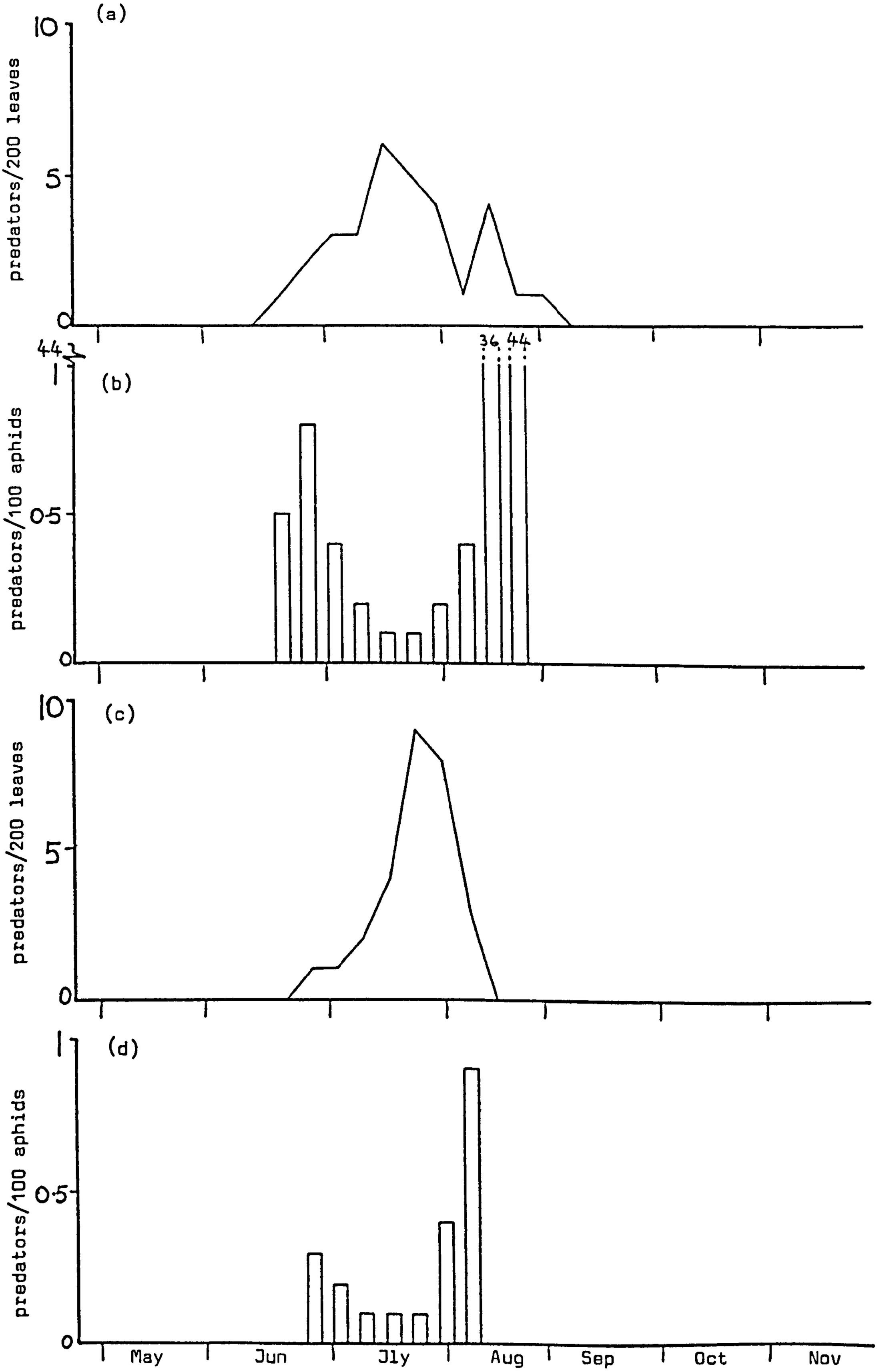

(a)
10
5
0
predators/200 leaves
44
36
44
(b)
predators/100 aphids
5
0
(c)
10
5
0
predators/200 leaves
(d)
1
0·5
0
predators/100 aphids
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 119 :

Relative abundance of predators, WM 110,

section 2, 1983

(a) 3.5 m

(b) 7.5 m

(1) Coccinellidae

(2) Anthocoridae

(3) B.angulatus

(4) O.marginalis

(5) P.ambiguus

(6) Neuroptera

(7) Syrphidae

(8) Cecidomyiidae

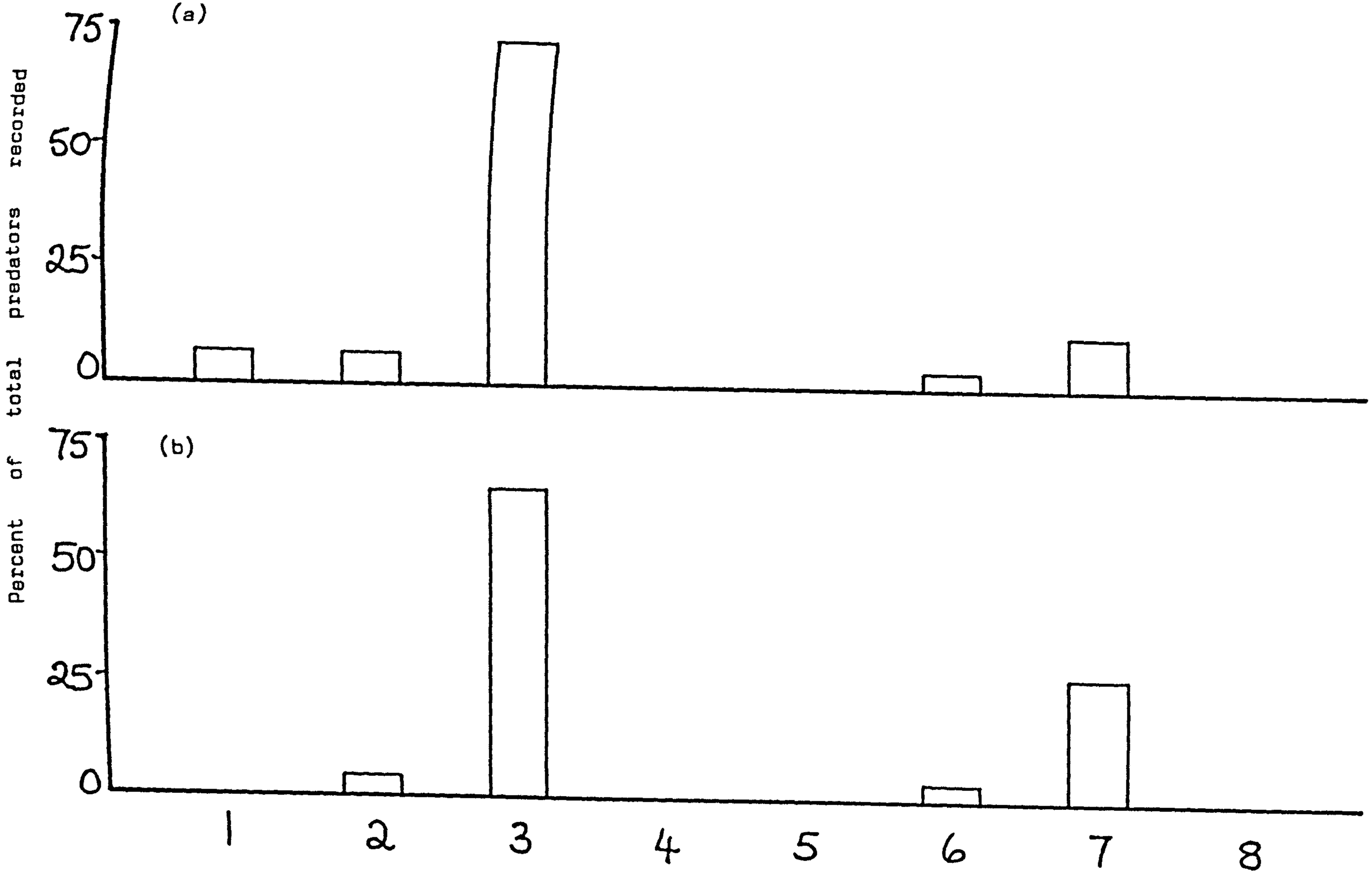

(a)
75
50
25
0
Percent of total predators recorded
(b)
75
50
25
0
1
2
3
4
5
6
7
8

Figure 120:

Numbers of B.angulatus on WM 110, Section 2, 1983

(a) 3.5 m

(b) 7.5 m

Nymphs

Males

Females

Figure 121:

Parasitism in populations of P.alni on WM 110, section 2, 1983

(a) 3.5 m

(b) 7.5 m

(a)
8
4
0
Number of B.angulatus per 200 leaves
(b)
8
4
0
Number of B.angulatus
(a)
8
4
0
Percent of aphids parasitized
(b)
8
4
0
May
Jun
Jly
Aug
Sep
Oct
Nov

section (for 3.5m,d=0.51, $p > 0.05$; for 7.5m,d=0.81, $p > 0.05$). Parasitism occurred until mid August (fig.121). No examples of aphids killed by fungi were recorded.

2.5.12 Vertical distribution of aphids, 1984

(i) Abundance of aphids

The trees within the tower were cut manually at the same time as the rest of section 2, in late January.

As occurred with the whole section aphid numbers in early spring were very low. Fundatrices were found at 3.5m but not at 7.5m. Numbers began to increase with the onset of reproduction by the second generation adults in late June -early July (figs.122a,123a). Numbers peaked at both heights on August 2nd, at the same time as on the whole section. Maximum numbers attained at 3.5m were similar to the whole section ($d=0.85, p > 0.05$) but were lower at 7.5m ($d=2.24$, $p < 0.05$) (table 30). After peaking numbers declined sharply, following similar patterns to the whole section. The pattern of abundance on terminal leaves was again similar and mirrored that of the population at both heights (figs.122b,123b). As in 1983, the density of aphids was greatest on terminal leaves for most of the season.

Instars I-III accounted for over 60% of the populations for most of the season. Proportions decreased late in the season when aphid numbers were low and greater proportions of alate and apterous adults occurred. Generations were the same as those found on the whole section, that is the second generation was apterous with some alatae being produced in the third and fifth. The fourth was entirely alate and the sixth apterous. The sexual forms represented the seventh generation. Again the age structures were different on terminal and non terminal leaves. Fourth instars (presumptive alatae) comprised a greater proportion of the population on

Figure 122:

Aphid populations at 3.5 m on WM 110

Section 2, 1984

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

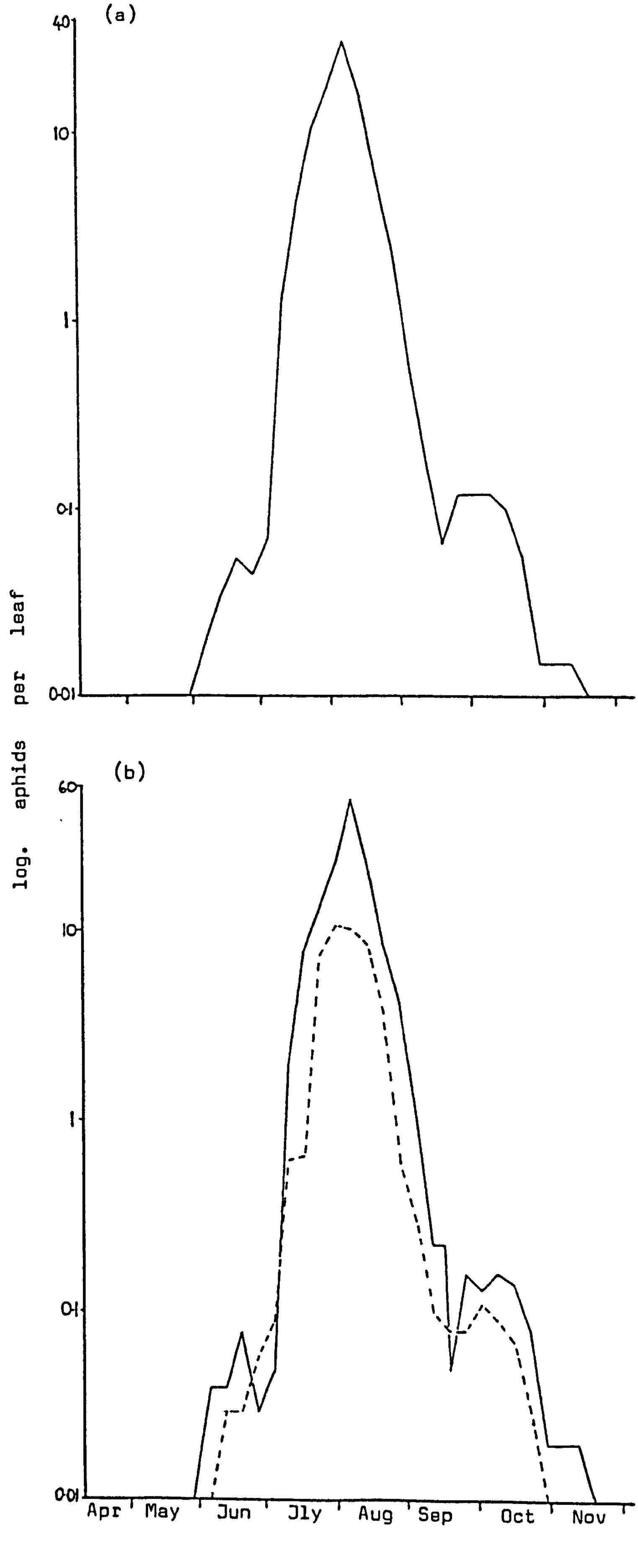

(a)
40
10
1
0·1
(b)
6
10
1
0·1
0·01
log. aphids per leaf
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 123:

Aphid populations at 7.5 m on WM 110,

section 2, 1984

(a) 200 leaf sample

(b) 100 leaf samples

- - - Terminal leaves

——— Non-terminal leaves

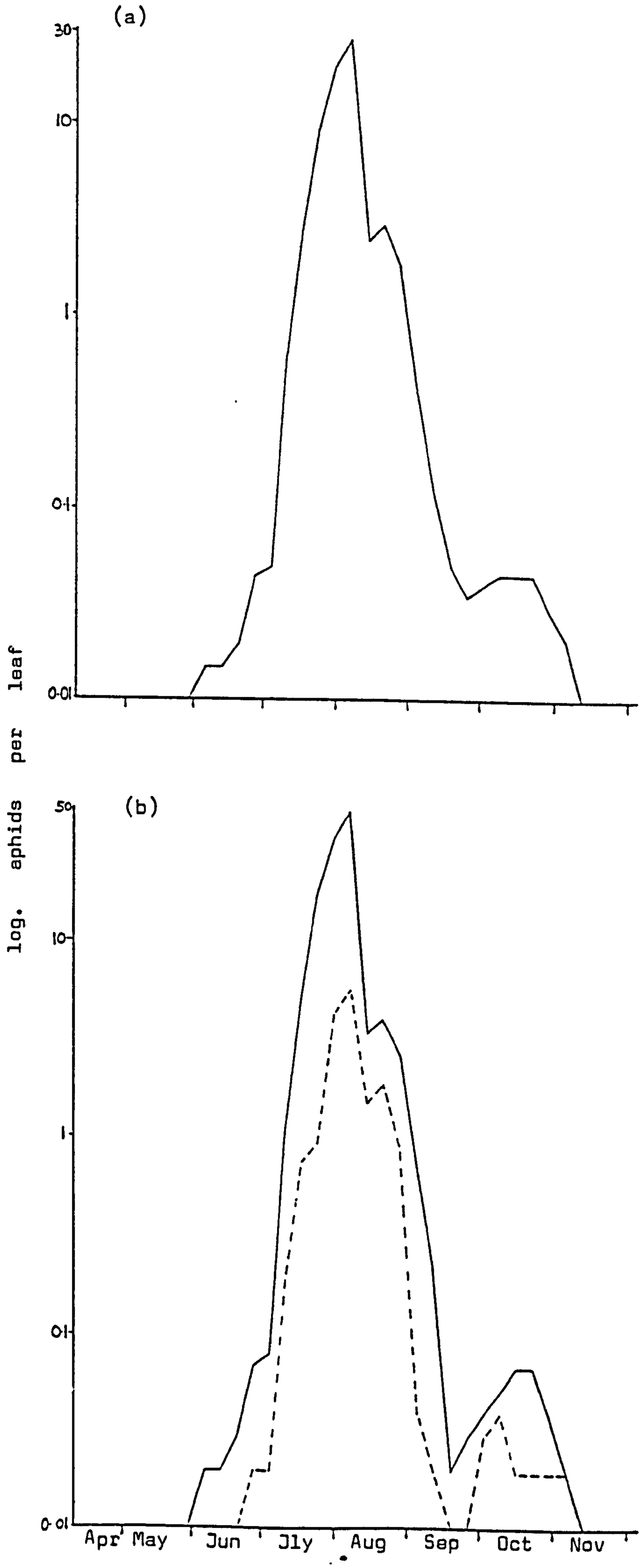

(a)
30
10
1
0·1
0·01
log. aphids per leaf
(b)
50
10
1
0·1
0·01
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Table 30 TOTAL NUMBERS OF APHIDS IN SAMPLES - VERTICAL DISTRIBUTION, EAST MALLING 1984

		3.5 m			7.5 m		
		Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample	Aphids/100 Terminal leaves	Aphids/100 Non-terminal leaves	Aphids/ Whole sample
April	26	0	0	0	0	0	0
May	3	0	0	0	0	0	0
	10	0	0	0	0	0	0
	17	0	0	0	0	0	0
	24	0	0	0	0	0	0
	31	0	4	4	0	1	1
June	7	3	0	3	0	1	1
	14	3	8	11	0	2	2
	21	6	3	9	2	7	9
	28	9	5	14	2	8	10
July	5	62	175	237	18	107	125
	12	64	786	850	76	501	577
	19	746	1334	2080	92	1760	1852
	26	1061	2366	3427	424	3428	3852
Aug	2	1012	5230	6242	559	4841	5400
	9	849	2371	3220	149	341	490
	16	371	836	1207	187	403	590
	27	147	424	483	88	272	360
	30	19	105	124	4	74	78
Sept	6	10	25	35	1	23	24
	13	8	5	13	0	1	1
	20	8	6	14	0	2	2
	27	11	3	14	2	3	5
Oct	5	9	6	15	3	3	6
	12	7	4	11	1	6	7
	19	3	3	6	1	6	7
	26	1	0	1	1	3	4
Nov	2	1	0	1	1	1	2
	9	1	0	1	0	0	0
	16	0	0	0	0	0	0
	23	0	0	0	0	0	0

terminal leaves and alate adults a greater proportion on non terminals. Proportions of nymphs, fourths (presumptive apterae) and adults tended to be greater on terminals (appendix 2.14,2.15).

Alatae were first produced in mid July, a month later than in 1983 (fig.117). At the time of the population peaks on August 2nd the fourth instar was entirely presumptive alatae. Alatae continued to be produced until the end of August. Proportions were similar at each height and to those of the whole section (fig.107).

Males and oviparae were produced during October. Ovipara numbers were low and there were no significant differences in abundance between heights ($t=0.61$, $d.f.=10$, $p>0.05$) or between these and the whole section (3.5m, $t=0.64$ $d.f.=10$, $p>0.05$; 7.5m, $t=1.54$, $d.f.=10$, $p>0.05$).

(ii) Spatial distribution of aphids

All values of b were significantly greater than unity (table 28) indicating that the aphids were aggregated, taking the season as a whole. The values of Morisita's index again showed the same trend as in previous samples (table 31).

(iii) Abundance of natural enemies

Predators were similar in abundance at both heights to the whole section (3.5m, $d=1.44$, $d.f.=35$, $p>0.05$; 7.5m, $d=1.68$, $d.f.=33$, $p>0.05$) and were similar between the heights ($t=0.32$, $d.f.=46$, $p>0.05$). Total numbers are shown in fig.124 a,c. The ratio of predators to aphids fell to 1 per 1000 at the time of peak aphid numbers, rising to 1 per 8 aphids at each height in early September (fig.124b,d,). B.angulatus was the commonest predator, accounting for 58% of numbers at 3.5m and 73% at 7.5m. Adults of A.nemorum and larvae of S.ribesii and E.balteatus were found at both heights whilst larvae of A.bipunctata and C.carnea only at 3.5m. Nymphs

Table 31 MORISITA'S INDEX OF DISPERSION AT 3.5M & 7.5M, 1984

Date		3.5 m		7.5 m	
		Terminal leaves	Non-terminal leaves	Terminal leaves	Non-terminal leaves
April	26				
May	3				
	10				
	17				
	24				
	31		20.0		0
June	7	0			0
	14	0	40.0		0
	21	12.2	18.6	0	14.1
	28	15.1	12.4	0	18.2
July	5	10.1	10.0	40.0	8.1
	12	9.8	8.3	29.3	6.3
	19	6.1	4.1	14.1	2.9
	26	3.2	3.1	6.2	2.4
Aug	2	3.4	2.6	6.3	2.5
	9	4.1	3.3	5.1	4.0
	16	4.0	3.9	5.3	3.8
	27	5.5	4.6	8.1	3.9
	30	11.1	6.3	0	11.1
Sept	6	20.0	11.1	0	8.2
	13	32.4	0		0
	20	33.3	0		0
	27	10.1	0	0	0
Oct	5	11.1	0	0	0
	12	0	0	0	0
	19	0	0	0	0
	26	0		0	0
Nov	2	0		0	0
	9	0			
	16				
	23				

Figure 124:

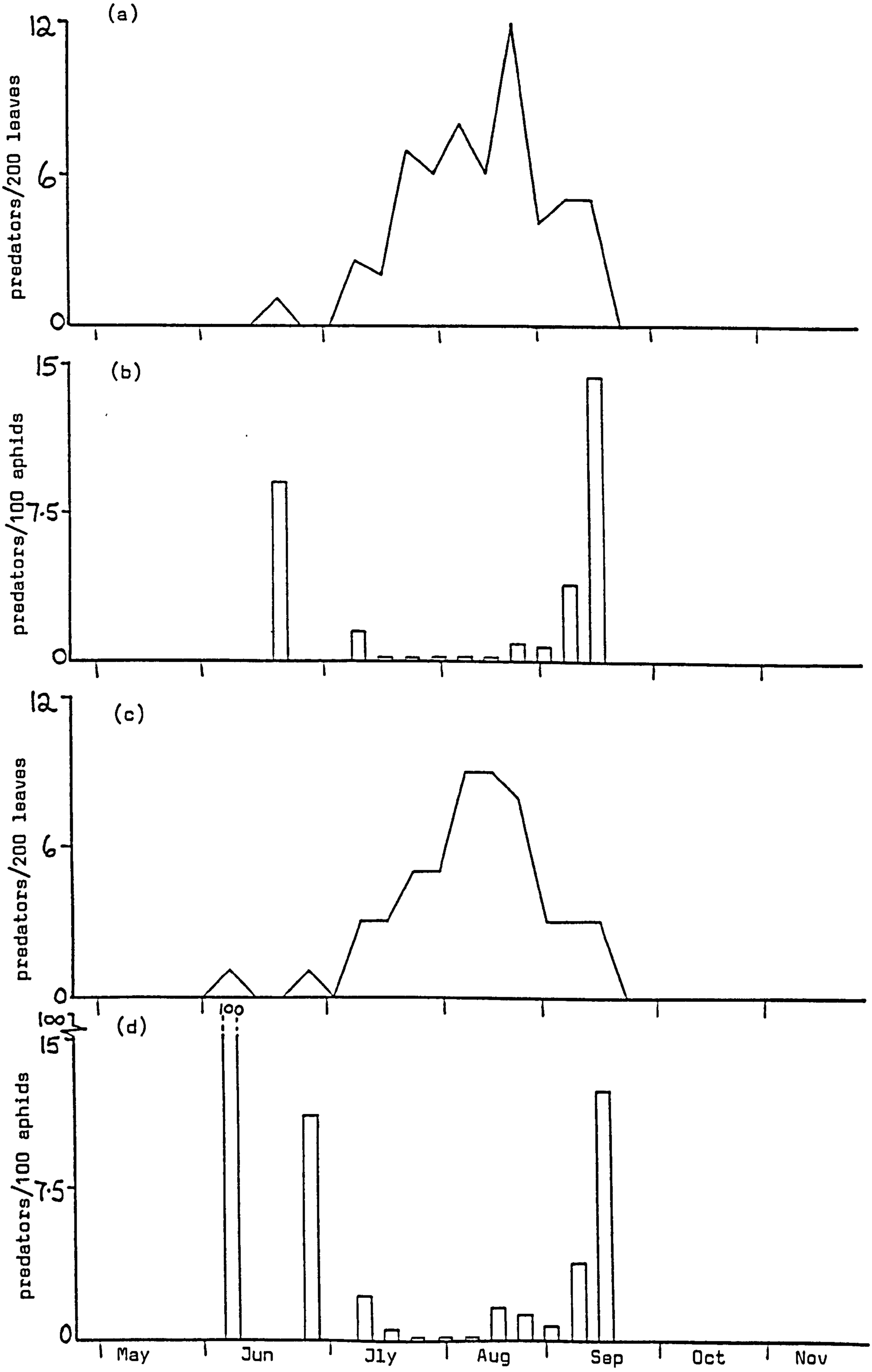
Abundance of predators on WM 110, Section 2 1984

(a) Total numbers of predators,3.5 m

(b) Ratio of predators to aphids,3.5 m

(c) Total numbers of predators,7.5 m

(d) Ratio of predators to aphids,7.5 m


(a)
12
6
0
predators/200 leaves
(b)
15
7·5
0
predators/100 aphids
(c)
12
6
0
predators/200 leaves
100
(d)
15
7·5
0
predators/100 aphids
May
Jun
Jly
Aug
Sep
Oct
Nov

of 8.angulatus appeared in early July and adults were present from early August until mid September. (fig.125).

Parasitism by T.pallidus was first observed in early July and reached a maximum rate of 9.8% at 3.5m and 5.1% at 7.5m (fig.126). The value for 7.5m was significantly different from that on section 2, but that for 3.5m not so, (3.5m,$d=0.92$, $p>0.05$; 7.5m,$d=2.27$, $p<0.05$). No examples of aphids killed by fungi were recorded.

2.5.13 The between year population dynamics of P.alni on WM110 and WM109

Tentative conclusions may be drawn on the three years' data available. More reliable information would be gained from a longer term study, but certain trends have emerged.

The results of the section of windbreak (section 2) which as closely as possible resembled the 'natural situation' of alder at Lyne will be considered first and then the effects of pruning, on sections 1 and 3 discussed.

The pattern of abundance was similar, although the numbers attained and the time of these peaks varied between the years. Fundatrices were commoner in 1983 than in 1982 and in 1984 numbers were so low that none could be found. Although the spring of 1982 was generally warmer than that of 1983 (fig.67), this did not appear to have such an effect on population increase as it did at Lyne. For the greater part of May 1983 the population growth rate was steady and greater for the corresponding time in 1982 (table 32). In late May 1983 the relative population growth rate per day was 0.15 (doubling time 4.6 days) compared to 0.04 (doubling time 17.3 days) in 1982. This appears to have been due to the greater numbers of fundatrices present. The population began to increase rapidly with the onset of reproduction by the second generation adults in 1982.

Figure 125:

Numbers of B.angulatus on WM 110

Section 2, 1984

(a) 3.5 m

(b) 7.5 m

Nymphs

Males

Females

Figure 126:

Parasitism in populations of P.alni on WM 110

Section 2, 1984

(a) 3.5 m

(b) 7.5 m

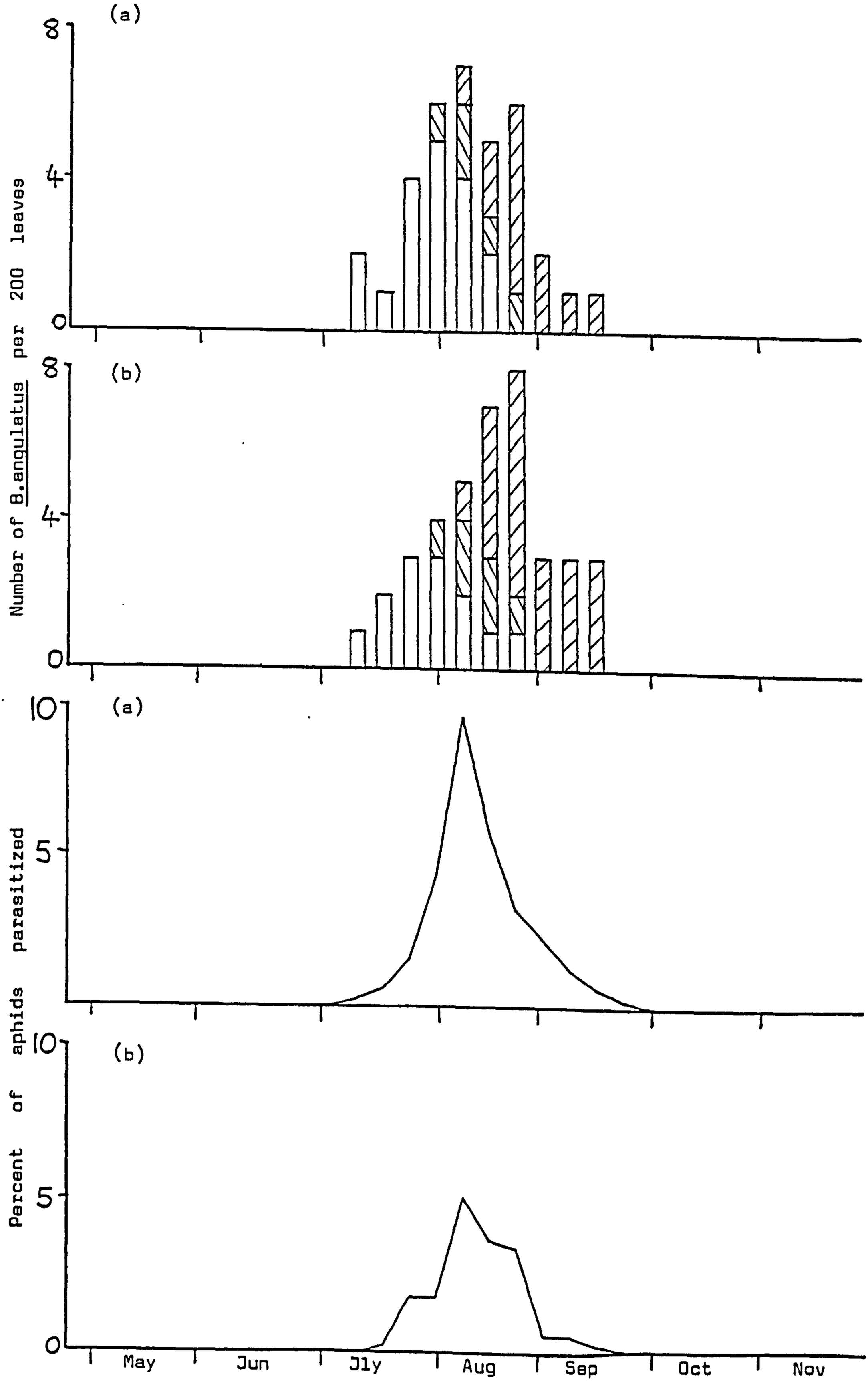

(a)
8
4
0
Number of B.angulatus per 200 leaves
(b)
8
4
0
(a)
10
5
0
Percent of aphids parasitized
(b)
10
5
0
May
Jun
Jly
Aug
Sep
Oct
Nov

Table 32 Relative Population growth rates per day $\left[(\ln N_2 - \ln N_1)\ (t_2 - t_1)^{-1}\right]$ during period of population growth -WM110 & 109

	1 9 8 2				1 9 8 3						1 9 8 4				
	WM110	WM109	WM109		WM110	WM110	WM110	WM109	WM109		WM110	WM110	WM110	WM109	WM109
Date	(1+2)	A	B	Date	1	2	3	A	B	Date	1	2	3	A	B
29/4- 6/5				28/4- 5/5	0.10	0.21	0.21	0.19		26/4- 3/5					
6/5-13/5	-0.10			5/5-12/5	-0.10	-0.06	-0.08			3/5-10/5					
13/5-20/5	0.31			12/5-19/5	0.07	0.16	0.06			10/5-17/5					
20/5-27/5	0.04			19/5-26/5	0.24	0.15	0.25			17/5-24/5					
27/5- 3/6	0.09			26/5- 2/6	0.12	0.11	0.02			24/5-31/5					
3/6-10/6	0.20	-0.16		2/6- 9/6	0.12	0.09	0.01			31/5- 7/6		0.43			
10/6-17/6	0.05	0.19		9/6-16/6	0.12	0.01	0.13			7/6-14/6	0.10	0.16			
17/6-24/6	0.12	0.12		16/6-23/6	-0.09	0.09	0.15	0.12		14/6-21/6	0.06	-0.08			
24/6- 1/7	0.14	0.02		23/6-30/6	0.12	0.07	0.10	0.08	-0.10	21/6-28/6	0.23	0.33		0.21	
1/7- 8/7	0.05	0.04		30/6- 7/7	0.22	0.18	0.14	0.09	0.37	28/6- 5/7	0.34	0.25	0.32	0.09	0.28
8/7-15/7	0.07	-0.01		7/7-14/7	0.14	0.14	0.06	0.27	0.23	5/7-12/7	0.16	0.19	0.10	0.14	0.17
15/7-22/7	0.07	-0.08		14/7-21/7	0.09	0.04		0.21	0.11	12/7-19/7	0.02	0.19	0.03	0.09	0.12
22/7-29/7	0.002	0.19	0.41	21/7-28/7					0.04	19/7-26/7	0.17	0.01	0.13	0.08	0.10
29/7- 5/8		0.36		28/7- 4/8						26/7- 2/8	0.09	0.04	0.07		-0.06
Over total period	0.09	0.02			0.09	0.10	0.09	0.07	0.13		0.14	0.14	0.13	0.10	0.09

This was also the case in 1984, where numbers were increased by the arrival of alates from other alder and their subsequent reproduction. The finding of alate adults before fourth instar nymphs (presumptive alatae) may have been due to sampling error in not finding nymphs in the leaf samples, or the arrival of alatae from other alder. It seems unlikely that winged individuals were produced at this time due to the low population density (section 2.5.9). The alates present were reproducing and it is shown in chapter 3 that newly moulted alate adults contain no embryos within their bodies but that these are matured later. Thus it seems likely that these alates were colonizers from other alder.

The overall relative growth rates for the populations were similar in 1982 and 83 but greater in 1984 (table 32). The cause of the higher value for 1984 was that the period of increase of the population was less than for the previous years (nine weeks compared to twelve).

Winged individuals were first found on June 16th in 1983, earlier than in 1982 (July 1st) and 1984 (July 5th). This is a likely result of the higher aphid density in 1983, alates appearing in the second generation in that year, whereas none were produced until the third generation in 1982 and 1984.

Ovipara numbers were less in autumn 1983 than in 1982 or 1984 (table 33). This is similar to the observations at Lyne where relatively high numbers of fundatrices resulted in lower numbers of oviparae and vice versa. A significant negative relationship occurred at Lyne, but this could not be accurately tested here, due to having only three data points. However these results do suggest that a similar relationship existed at East Malling.

Section 3 was pruned in summer 1982, before the population peaked. The population was considerably reduced (table 15, fig.69), but numbers of oviparae were greater than on section 2 (table 33). As a consequence

Table 33 PEAK NUMBERS OF FUNDATRICES AND OVIPARAE RECORDED IN 200 LEAF SAMPLES - EAST MALLING, 1982,83 & 84

		WM 110			LF125	
		SECTION			SECTION	
		1	2	3	1	2
Spring 1982	Fundatrices	2	2	2	13	13
Autumn 1982	Oviparae	11	11	22	38	38
Spring 1983	Fundatrices	4	4	12	68	68
Autumn 1983	Oviparae	1	3	1	14	6
Spring 1984	Fundatrices	0	0	0	21	13
Autumn 1984	Oviparae	20	8	18	10	7

Table 34 EFFECT OF PRUNING ON APHID POPULATIONS

Section & Date		Weeks Relative to Aphid Peak i.e. Pruning Date	Ratio of Pruned/ Unpruned - Population Peak	Ratio of Maximum Oviparae Numbers Pruned/Unpruned
WM110:3	1982	- 1	0.60	2.00
WM110:1	1983	+ 1	0.95	0.33
WM110:3	1983	+ 2	0.67	0.33
WM110:1	1984	- 3	0.51	2.50
WM110:3	1984	- 3	0.24	2.25
LF125:2	1983	+ 4	1.00	0.43
LF125:2	1984	+ 2	1.37	0.70

fundatrices were commoner and the population increased rapidly in spring 1983. Peak numbers were less than on section 2 ($d=3.27$, $p<0.01$) and were attained a week earlier.

Ovipara numbers on section 1 were similar to those on section 2 in autumn 1982. Pruning of section 2 during winter did not appear to affect the subsequent spring numbers of fundatrices and these were similar (table 33). The two populations peaked on the same day in 1983, attaining similar levels ($d=-0.38$, $p>0.05$) and declined at the same time. Overall population growth rates of the three populations were very similar (table 32). Although the numbers on 3 were less than on sections 1 and 2, these were attained in a shorter time interval.

Ovipara numbers in 1983 were lower than in 1982 (table 33). There was some evidence that oviparae were commoner on section 2 but this was not proven satisfactorily ($d=1.74$, $p>0.05$). No fundatrices were found on any section in 1984 and all populations attained their peak levels later than in 1983, on August 2nd. Sections 1 and 3 were pruned before the populations peaked and although this checked the increase, the growth rate assumed its previous values afterwards (table 32). Overall growth rates were similar. The population level attained on section 2 was greater than on section 1 ($d=5.18$, $p<0.001$) and this in turn was greater than on section 3 ($d=5.94$, $p<0.001$). Subsequent ovipara numbers were similar on sections 1 and 3 but less on section 2 (table 33)

As with LF125, aphids were considerably more common than at Lyne, peak numbers on WM110 generally being 30-40 times greater. Patterns of abundance were similar however, with a tendency for populations to oscillate in numbers from year to year becoming apparent. The numbers of oviparae and fundatrices fluctuated in a similar manner to those at Lyne but these fluctuations appeared to be modified by the pruning of the windbreak.

Timing of the pruning relative to the population peak was important and a summary of the results on the pruned sections relative to their controls is given in table 34.

The age structure of the populations at their peaks is given in table 35. Comparison of this with table 7 for Lyne shows that at East Malling, where population levels were higher, the proportion of apterous adults was considerably less and that of alatae considerably more than at Lyne. It seems likely that these results were caused by the large numbers of alatae produced due to crowding. If section 2 is considered in 1982,'83 and '84 there is some evidence to suggest that regardless of population size a relatively low population contains higher proportions of apterous adults and lower proportions of alate adults than a high population, as at Lyne. Other sections whose peaks were not affected by summer pruning may also be considered in this analysis. WM110 sections 1 and 3 in 1983 and LF125 sections 1 and 2 in 1983 and 1984 also tend to support this finding.

It was noticeable that a consistent difference emerged in the age structure on terminal and non terminal leaves (appendix 2). Fourth instars (presumptive alatae) formed greater proportions of the population on terminal leaves but alate adults were greater on non-terminals. It has been reported that in all cases, during population build-up, the aphid density was greatest on terminal leaves. Thus it seems likely that the increased density caused increased alata production and subsequent flight. On non-terminal leaves aphids were more widely spaced resulting in more apterae being produced and a reduced tendency to fly by the alatae.

Aphid abundance at 3.5m and 7.5m followed very similar patterns to that of the main section of windbreak sampled. However, when fundatrix numbers were similar, the population levels attained at 7.5m were consistently lower than those on the whole section. Predator numbers tended to be

Table 35 AGE STRUCTURE OF POPULATIONS AT THEIR PEAKS, - EAST MALLING, 1982, 1983 & 1984

Windbreak & date	Population Peak - Aphids/leaf	Nymphs	% IV Apterae	Apterous Adults	IV Alatae	Alate Adults
WM110:1,1982	16.38	86.3	0.3	0.7	8.1	4.6
WM110:1,1983	41.56	81.4	0.0	0.1	7.6	10.9
WM110:2,1983	43.80	75.5	0.0	0.2	8.9	15.4
WM110:3,1983	29.36	56.8	0.0	0.4	16.5	26.3
WM110:1,1984	17.20	72.1	0.2	0.1	8.0	19.6
WM110:2,1984	34.00	71.3	0.0	0.3	11.7	16.7
WM110:3,1984	8.27	75.2	0.0	0.5	7.6	16.7
LF125:1,1983	27.83	61.7	0.0	0.5	26.4	11.4
LF125:1,1984	13.63	77.7	0.0	0.7	13.0	8.6
LF125:2,1984	18.74	75.7	0.0	0.5	12.8	11.0

lower at 7.5m but this was not proven statistically. The populations attained at 3.5m showed no significant differences to those of the whole section. Ovipara numbers were low but no consistent differences emerged with the change in height.

2.6 DISCUSSION

2.6.1 Population dynamics of P.alni

The pattern of abundance on the windbreaks at East Malling appears to have been determined by similar factors to those which influenced the aphid populations at Lyne.

The rate of increase of the population in spring is influenced by the number of fundatrices present. The effect of temperature, which at Lyne affected the early season increase in numbers, did not have a great influence at East Malling. It is likely that the greater number of fundatrices present masked any temperature effects. When high numbers of fundatrices emerged from overwintering eggs the population peak attained was earlier in the season than when fundatrix numbers were low. At Lyne these 'early' populations were lower at their peak levels than later populations. At East Malling, early peaking populations tended to be higher than later ones. Numbers were so much higher than at Lyne (about 30 times) that high aphid numbers in spring caused the reproduction of the first and second generations and the subsequent population peak to be very high. When numbers were lower in spring, fewer aphids were produced and the numbers attained less.

Alate adults were produced in the second and third generations at East Malling. As these became more crowded they flew away, as shown by sticky trap catches (chapter 3). Eventually a point was reached where reproduction ceased, the nymphs matured into alate adults and these migrated. This

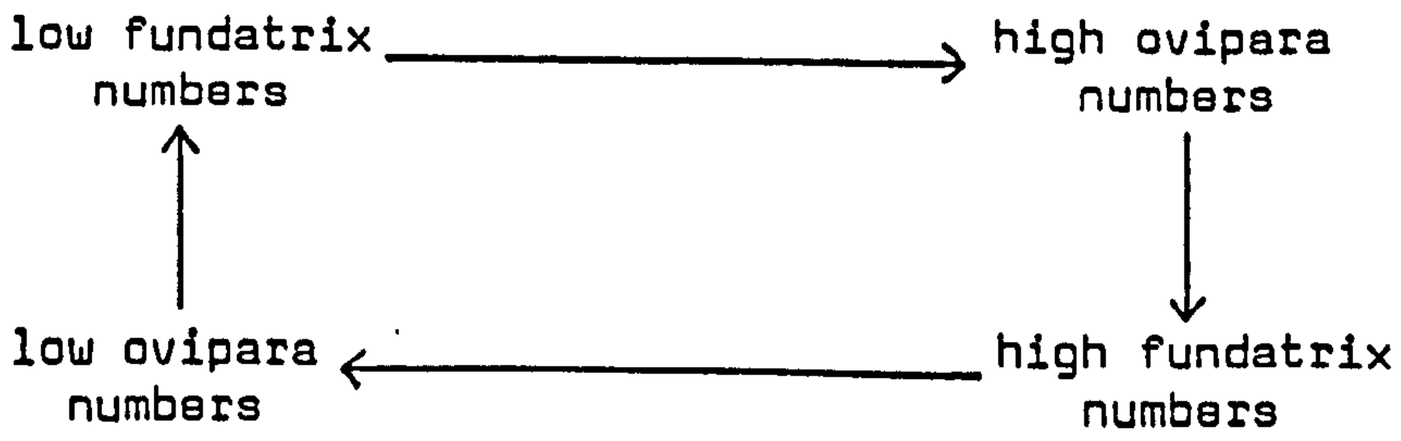
caused the population to decline, the same situation as occurred at Lyne. The extent and nature of the peaks was determined by the number of fundatrices present in spring. Higher numbers of fundatrices meant that more aphids were produced and more present when the migration occurred. Lower numbers meant a slower population growth rate so that peak numbers occurred later in the season and were lower, because of the smaller number of aphids produced. Even when the numbers at East Malling were 'low' they were still considerably higher than those at Lyne.

The situation is complex at East Malling because all windbreaks have to be pruned and so no section is directly comparable to the branches at Lyne. Section 2 on WM110 is most similar and was not cut in summer, only in winter. Population peaks alternated between years with the highest peak resulting from the highest number of fundatrices. Populations of aphids were similar at 3.5m to the whole section samples taken between 0 - 1.5m, but there were lower populations at 7.5m, even when these resulted from similar fundatrix numbers in spring. It is possible that the food quality of leaves was poorer at 7.5m but this was not measured. Higher numbers of non alate aphids were recorded upon sticky traps at 7.5m than 3.5m (chapter 3) and so it is likely that wind was a major factor restricting population increase at this height.

The seasonal pattern of abundance is determined by several factors. The spring numbers of fundatrices determine the rate of increase and size of the population peak. The subsequent decline is caused by the cessation of reproduction, maturation of nymphs into alatae and the migration of these alates from the windbreak. The peak occurs early in the season if fundatrix numbers are relatively high; later if they are low. This is a very similar situation to that reported for other tree dwelling aphids such as E.tiliae on lime (Dixon,1971c) and C.juglandicola on walnut (Sluss 1967). Post peak development of populations is likely to be affected by

predators, mainly female B.angulatus which tend to remain on the windbreaks whilst the males fly away. On LF125 in 1982 aphid populations increased from very low levels in mid summer to produce large numbers of oviparae in autumn, when predators were scarce. Subsequent recoveries from low levels were not so marked in 1983 and 1984 when predators were more abundant.

The spraying of LF125 in 1982 provides a rather extreme example of how large numbers of oviparae develop from a relatively low population peak. The reproduction of apterous summer generations and the relative scarcity of predators resulted in higher numbers of oviparae in autumn 1982. These resulted in high numbers of fundatrices in spring 1983. The population attained was higher and subsequent ovipara numbers lower than that of the following year, 1984, when fundatrices were less common (table 33). E.tiliae shows similar changes in ovipara numbers after high and low population peaks (Dixon,1971c). After low,late population peaks (resulting from low numbers of fundatrices) large numbers of oviparae were produced. The converse was also true. At Lyne, a strong relationship existed between the number of oviparae in a year and fundatrices the following spring (p.) and a negative relationship between fundatrices and oviparae in the same year. Thus the tendency is:



The timing and extent of the population peak is influenced by spring numbers of fundatrices and thus by numbers of oviparae resulting from the previous year's population. Pruning drastically affects the aphid

populations present and thus the subsequent numbers of oviparae and fundatrices. When a windbreak was pruned before the aphid population reached its peak, the aphid numbers attained were less than those on the corresponding unpruned section. If pruning occurred after the population peaked, levels were obviously unaffected and were generally similar (table 34). Differences in the numbers of oviparae produced were also noticed. When pruning occurred before the population peak, more oviparae were produced on the cut section. When pruning occurred after the peak, oviparae were less common (table 34). When pruning occurred close to the population peak (WM110 section 3, 1982) numbers declined prematurely. Those alates remaining did not fly but began to produce late summer generations which were apterous and these in turn gave rise to the oviparae. When pruning occurred as the population was increasing rapidly, (WM110 sections 1 and 3, 1984) numbers were checked and the subsequent peak was smaller but at the same time as the uncut section. On these cut sections, reproduction by the late summer generations which were commoner because of less migration by the previous alate generations gave rise to the increased numbers of oviparae relative to the 'control' section.

When pruning occurred after the population peaked (WM110 sections 1 and 3 1983, LF125 section 2, 1983 and 1984) the declining numbers were reduced still further and less aphids remained on these sections. Fewer oviparae were produced as a result of fewer numbers of apterous late summer generations.

Whether or not a windbreak is pruned, the populations tend to oscillate from year to year with high ovipara numbers in one year being followed by low in the next and so on. The pruning appears to modify these numbers, rendering them more extreme (table 34). Due to pruning taking place at the convenience of the contractors, not all combinations of pruning time and population peak time could be investigated. It would be interesting

to examine the effect of early pruning on an early peaking population. One might expect higher numbers of oviparae produced due to the early, artificial reduction of aphid numbers, and thus modify the 'high fundatrix numbers giving low ovipara numbers' situation to 'high gives high'. However, in any investigation of this kind consistency of results through repetition is of paramount importance. Pruning before a late population peak was achieved three times, after an early one three times and after a late one, once. Results did indeed show a consistent trend (table 34). Early pruning produced more oviparae relative to controls and late pruning less. The population timing and level in any one year may thus be altered by cultural control of the host and population manipulation in the previous year. The disruption of a habitat at critical times and its effect on insect abundance was reported for the weevil Zacladus geranii (Payk) on the meadow cranesbill Geranium pratense L. (Davis, 1973). Cutting this plant between June and the end of August disrupted larval development within the seeds. Perrin (1974) recorded the effects on populations of the aphid M.evansi of cutting patches of its stinging nettle host. Patches cut before aphid population peaks in May and June resulted in recolonization of plots on the regrowth of stems. Patches cut when aphid numbers were declining showed no subsequent increase. These situations are similar to the pruning of alder but in this study a substantial proportion of the host remains instead of complete removal. Aphid populations reduced early in the season have the facility to respond immediately. Those reduced later are simply further depleted by the action of pruning.

2.6.2 The advantages of polymorphism in P.alni.

The production of apterous and alate forms in P.alni is in contrast to that of all other members of the Callaphididae whose population dynamics have been studied. The fundatrix generation is always apterous and when numerous, alate individuals are produced in the second generation. When fundatrices are extremely scarce such as happened at Lyne in 1983 and on

WM110 at East Malling in 1984 alates are not produced until the third and fourth generations, later in the season. The high numbers present in spring cause high population peaks with the converse also being true. This occurred at East Malling and is very similar to the situation reported for the lime aphid (Dixon,1971). When fundatrix numbers are very low (e.g. 1 per 500 leaves as at Lyne in 1983) the pattern of abundance is different, with the later population peak being higher. This is due to reproduction by apterous adults of the second and third generations. Thus even when numbers are initially low the apterous adults result in high numbers in summer.

The production of apterous forms means that P.alni is able to adapt to changing circumstances in its habitat such as pruning at East Malling. Certain aphids such as D.platanoidis (Dixon,1963) and E.punctipennis (Wratten, 1974) undergo reproductive diapause in summer. Others, such as E.tiliae (Dixon 1971c) and T.annulatus (Lorriman,1980) show little increase in numbers after population peaks. The small, poor quality aphids present due to poor food quality and previous crowding means that increased reproduction does not occur. Generations of P.alni subsequent to population peaks are apterous and able to reproduce at a greater rate than their alate counterparts (chapter 5). After artificial reduction, numbers thus increase to a greater extent than in populations where the decline is caused by alate migration. M.evansi, studied by Perrin (1974) also exhibits facultative alate production and population changes of this aphid were most similar to P.alni.

Chapter 3. ALATE MORPH DETERMINATION AND FLIGHT IN P.ALNI

3.1. ALATE MORPH DETERMINATION

3.1.1. Introduction

Extensive research on the production of agamic winged forms in aphids has shown that several environmental factors, separately or in combination, may act in a variety of ways to influence the production of alatae. Early workers noted that alata-free generations were produced if colonies were kept sparse, but that alata numbers increased when population density on the host plant was allowed to rise (Ewing,1925, Ackerman 1926, Reinhard,1927). The effect of high population densities on alata appearance was generally attributed to partial starvation. The role of crowding or 'group effects' (l'effet de groupe) in influencing various activities in insects had been stated by Grassé (1946) but Bonnemaison (1951) working with M.persicae and B.brassicae first proposed the role of crowding, that is, the proximity of one aphid to another in alata production. Since this work numerous similar conclusions involving other aphids have been reached.

The positioning of the period responsive to crowding within the life cycle differs according to the aphid species. In Macrosiphoniella sanborni (Gillette the determination of winged forms is wholly embryonic and is controlled by maternal crowding reactions (Kitzmiller, 1950). Wing formation is also determined prenatally in M.viciae (Lees,1967), A.pisum (Sutherland, 1969a) and M.dirhodum (Elkhider, 1979). However, in Rhopalosiphum prunifoliae (Fitch) (Noda, 1958), Therioaphis maculata (Buckton) (Toba, Paschke and Friedman,1967) and C.fragaefolii (Judge and Schaefers, 1971) it operates postnatally through crowding of the first instar nymphs. This may also be true of B.brassicae (Kawada, 1965) although Bonnemaison (1951) thought that crowded first instar nymphs would not develop into alatae unless stimulated by the presence of parent aphids. Kidd and Tozer (1984) found that crowding operated postnatally in Cinara pinea Mordvilko but that this effect only occurred when the host tree was in the active stages of shoot

growth. Some species respond to both prenatal and postnatal crowding In this category Aphis craccivora Koch (Johnson,1965), M.persicae (Awram,1968, Sutherland and Mittler, 1971), A.fabae (Shaw 1970a) Rhopalosiphum padi (L). (Dixon and Glen, 1971), Rhopalosiphum insertum (Walker) (Dewar, 1976), Sitobion avenae (Fabricius) (Watt and Dixon,1981; Ankersmit and Dijkman, 1983) and Brachycolus asparagi Mordvilko (Tamaki et al, 1983) have been reported.

Other environmental factors have been shown to affect alata production. Temperature has been shown to influence A.craccivora (Johnson and Birks, 1960; Johnson, 1966b), M.viciae (Johnson,1966b, Lees 1967) and C.fragaefolii (Schaefers and Judge, 1971). In all these species, higher temperatures tended to suppress the production of alatae.

A reduction in photoperiod appeared to exert a prenatal effect in A.craccivora (Johnson 1966b) and C.fragaefolii (Schaefers and Judge 1971) but this response is of minor significance compared to crowding.

The quality of the host plant has also been shown to be important in influencing alata production in some species. Winged individuals are more commonly produced on relatively old, mature or senescent tissue in A.craccivora (Johnson and Birks, 1960; Johnson, 1965) B.brassicae (Hughes 1963) M.viciae (Lees 1967) (in this case indirectly through increased restlessness of aphids on mature leaf tissue and thus more tactile stimulation resulting in increased production of alatae), A.pisum (Sutherland, 1969b), C.fragaefolii (Schaefers and Judge,1971) and Sitobion avenae (Watt and Dixon, 1981). However, instances have been reported in which alate production coincides with optimal aphid performance on high quality foliage. Examples are C.pinea (Kidd and Tozer, 1984) and Elatobium abietinum (Walker) (Parry, 1977). E.abietinum has been shown to be responsive to many factors inducing alata formation. Fisher (1982)

found that crowding was not required for alata production if the host plant quality was suitable. Photoperiod was shown to act directly on the aphid whereas crowding and temperature exerted secondary effects.

In addition to the extrinsic factors listed above, certain intrinsic influences may also effect the production of alatae. The alate morph appears to produce fewer or no alatae compared to the apterous form. Crowded alatae of M.viciae (Lees 1966) A.fabae (Shaw 1970a) and A.pisum (Sutherland, 1970) do not produce alate offspring, whereas alatae of T.maculata (Toba et al, 1967) and M.dirhodum (Elkhider,1979) produce fewer than apterous parents. This occurrence in M.viciae and A.pisum has been attributed to an intrinsic factor which is time-dependent rather that generation-dependent, so that the morph in question could only be produced after a fixed passage of time, even though the number of generations might vary. Lees called this intrinsic mechanism an 'interval timer'. Burns (1972) discovered that in M.viciae, the proportion of alatae produced depended on whether the aphid had flown, however. In contrast to these aphids, alate forms seem to be readily produced from alatae in S.avenae (Watt and Dixon, 1981). There are marked clonal differences in some species. MacGillivray and Anderson (1958) found that certain clones of Aulacorthum solani (Kaltenbach) produce alatae abundantly whereas others never do so. Clonal differences have also been reported in A.pisum (Sutherland, 1969a) and S.avenae (Lowe, 1980)

In this section the response of P.alni to crowding is reported. Experiments with crowding and isolation of each generation, beginning with the fundatrix were carried out. The responses to crowding were examined throughout the reproductive life and changes in these together with the implications for population growth are discussed.

3.1.2. Materials and methods

Overwintering eggs were collected in early April and sections of twigs bearing eggs were placed in petri dishes with a slightly moist filter paper in an unheated outside shed. The dishes were examined daily and the hatched fundatrices used for experiments. In late April leaves of A.glutinosa are actively unfurling and growing and thus it was impossible to confine aphids within clip-cages of the type described by Noble (1958) for fear of damaging and killing the leaf. Aphids were confined upon leaves by coating the petioles in 'Oecotak' (Oecos Laboratories Ltd., Kimpton, Herts). Small pieces of branch bearing these leaves were enclosed in fine black muslin to guard against insect predators and to afford some protection from wind. When the aphids had reached the third instar in mid May, leaves were large enough to 'accept' cages, and these were applied enclosing the aphids present upon the leaves. Fundatrices were reared until adult in numbers varying from one to sixteen per cage. The offspring of these adults were then reared in groups or isolation and their morphs determined when adult. Fundatrices which had been crowded were isolated at the teneral adult stage. The reactions to crowding or isolation in mother and offspring throughout the mother's reproductive life could thus be examined. 'Batches' of offspring produced weekly were reared alternatively in crowded and isolated conditions. Isolated offspring were obtained by examining the cage twice daily. The young aphid produced in this time was left and the adult removed to another leaf and caged. This procedure was repeated for four days. During the subsequent three days cages were examined daily but all offspring produced were removed and killed. During the next four days the offspring of this aphid were crowded in a cage,thus: the cage was examined after two days and all offspring produced left and the adult removed and caged on another leaf. Therefore from each fundatrix in each batch there were two cages of crowded (between 2 and 7) offspring and between four and eight cages

of isolated offspring (some aphids producing two nymphs per day). No fundatrix lived for more than five weeks and so the maximum number of batches produced was five. Similar numbers of fundatrices which had been reared in groups were left in crowded conditions but isolated only for the four day periods to produce offspring. They were returned to the group for the intervening three day periods. The morphs of all aphids reared in groups and isolation were determined at adulthood. All aphids were reared in the field on windbreak LF125. Ten replicates of each treatment were performed, two on each of five branches selected at random from the windbreak.

3.1.3. Results

If the first batch of offspring produced by the fundatrices are considered, it is apparent that there were differences in the morphs produced under the different rearing conditions (table 36). The mean daily temperature during this experiment was 12.6^{o}C.

When fundatrices and their offspring were reared in isolation, no alatae were produced. Significantly more alatae were produced if these offspring were crowded (χ^2 = 6.79, $p < 0.01$), indicating that a postnatal response to crowding exists in P.alni. When fundatrices were crowded and their offspring isolated more alates were produced than when both were isolated (χ^2 = 15.62, $p < 0.001$) indicating that a prenatal response also exists. When fundatrices were crowded and their offspring isolated more alatae were produced than if the offspring only were crowded (χ^2 = 5.30, $p < 0.05$) suggesting that the prenatal response may have more effect than the postnatal response. When both fundatrix and offspring were crowded more alatae were produced than if only the fundatrix (χ^2=29.28, $p < 0.001$) or the offspring (χ^2= 89.14, $p < 0.001$) had been. The percentage mortality tended to increase with the degree of crowding. Even if all those that

Table 36 The effect of exposing fundatrices and offspring to crowding on the numbers of apterae (Ap) and alatae (Al) produced.

Fundatrix reared	Offspring reared	Number of aphids: Ap	Al	%Al	Mortality of offspring (%)
isolated	isolated	21	0	0	30.0
isolated	crowded	50	22	30.5	28.0
crowded	isolated	16	20	55.5	29.4
crowded	crowded	10	132	92.9	31.1

Table 37 The effect of exposing mothers and offspring of the first three generations to crowded (cr) and isolated (i) conditions on the numbers of apterae (Ap) and alatae (Al) produced

APTEROUS SECOND GENERATION

Fundatrix reared	2nd gen. reared	3rd gen. reared	Number of aphids: Ap	Al	% Al	Mortality of offspring (%)
i	i	i	34	1	2.8	18.6
i	i	cr	8	16	66.7	21.1
i	cr	i	3	57	95.0	40.0
i	cr	cr	3	63	95.4	28.3
cr	i	i	26	1	3.7	28.9
cr	i	cr	7	55	88.7	26.2
cr	cr	i	2	33	94.3	20.4
cr	cr	cr	2	103	98.1	19.2
ALATE SECOND GENERATION						
i	i	i				
i	i	cr				
i	cr	i	19	17	47.2	20.0
i	cr	cr	2	61	96.8	18.2
cr	i	i	23	0	0	32.5
cr	i	cr	16	34	68.0	29.6
cr	cr	i	11	11	50.0	45.0
cr	cr	cr	17	69	80.2	23.9

died were potential apterae crowding still had a significant effect upon alata production.

When fundatrices were crowded, there appeared to be no relationship between the number of offspring reared per cage and the proportion of alatae amongst them ($r= 0.290, d.f.=18, p > 0.05$). When the mothers were reared in isolation however there was a relationship between the number of offspring per cage and the proportion of alatae produced ($r=0.532$, $d.f.=18$, $p < 0.05$) (fig.127). The more intense the crowding, the higher the proportion of alatae produced.

When fundatrices were crowded throughout their development and then isolated at the teneral adult stage, there appeared to be a changing response in the mother (fig.128). In each successive batch, all isolated offspring from isolated mothers were apterous. Successive batches of crowded offspring whose mothers were isolated produced very similar proportions of alatae (fig.128a) suggesting that the responses of nymphs to crowding did not vary over the adult's reproductive life. However, the isolated offspring reared from mothers which had been crowded at first produced 50% alatae but after two weeks, only matured as apterae (fig.128b). A similar change occurred in crowded offspring from crowded mothers (fig.128c) and this appeared to level out at a similar rate to that obtained by crowding offspring from mothers reared in isolation. When mothers were not isolated at the teneral stage, their subsequent batches of offspring produced similar proportions of alatae throughout (fig.128d,e). Thus it is likely that the change in response is due to the isolation of the mother at the teneral stage, after previous crowding.

The offspring from the four treatments of the second generation were themselves reared crowded or isolated, in batches, in the same manner as described above. The forms of the third generation in the first batch

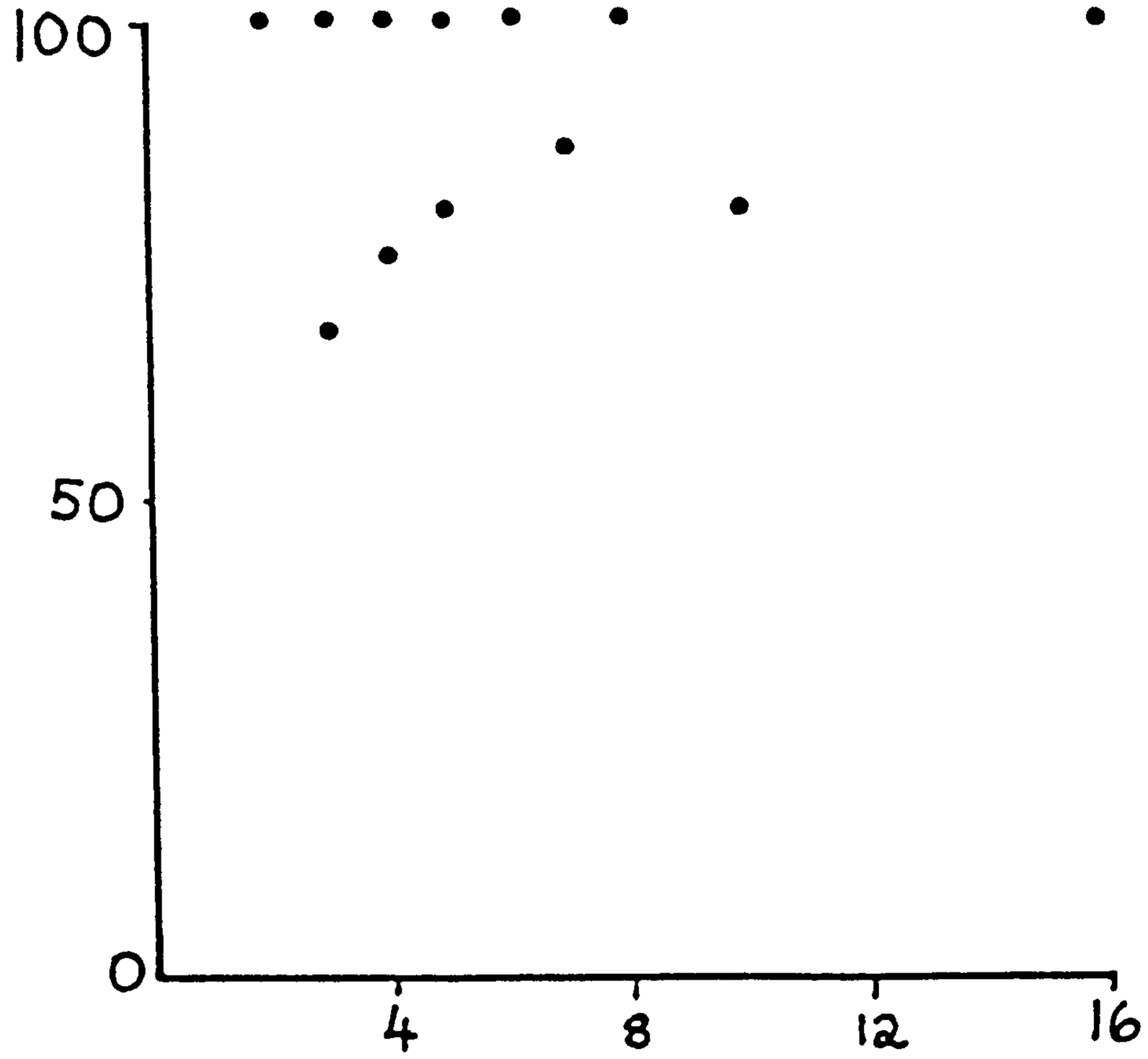
Figure 127:

Relationships between the number of second generation aphids reared per cage ($3 \cdot 1 cm^2$ of leaf) and the proportion of alatae amongst them

(a) Mother reared in crowded conditions

(b) Mother reared in isolation

(a)


100
50
0
4
8
12
16
Per cent of alatae reared per cage

(b)

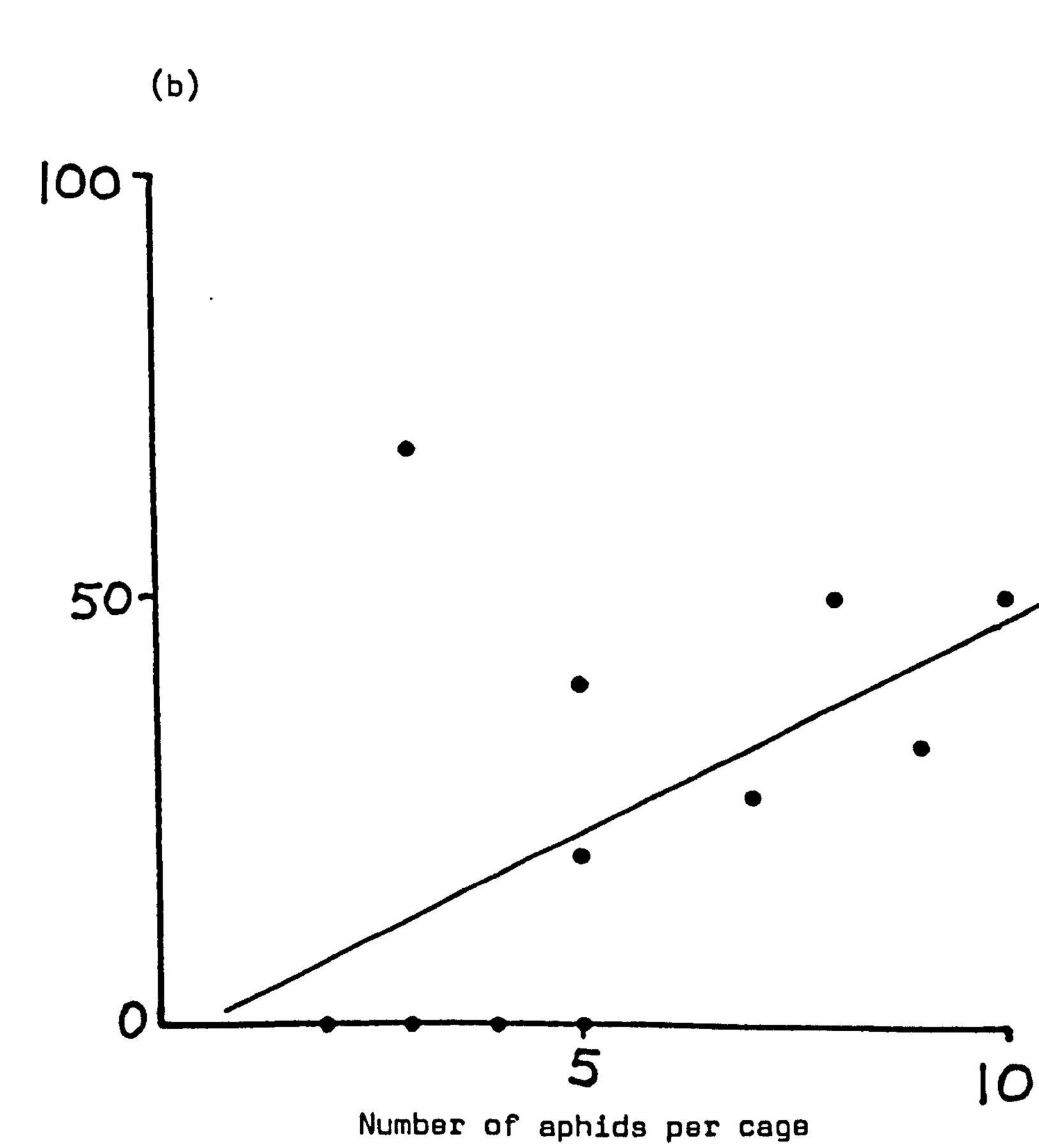

100
50
0
5
10
Number of aphids per cage

Figure 128:

The proportion of alatae in successive batches of offspring produced by fundatrices:

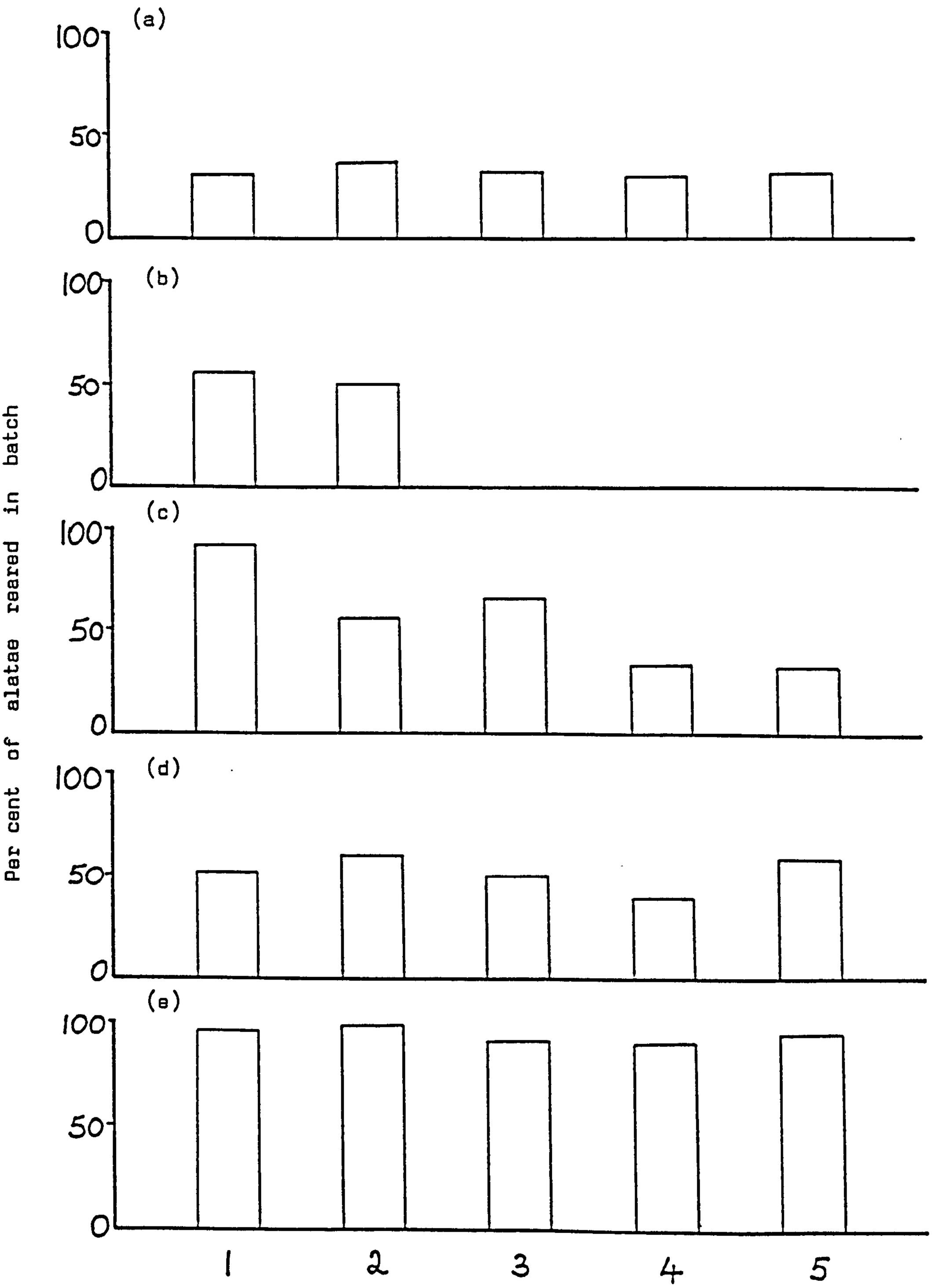
(a) Fundatrix reared in isolation, offspring crowded

(b) Fundatrix reared crowded, isolated at teneral stage, offspring isolated

(c) Fundatrix crowded, isolated at teneral stage, offspring crowded

(d) Fundatrix crowded throughout life, offspring isolated

(e) Fundatrix crowded throughout life, offspring crowded


(a)
100
50
0
(b)
100
50
0
(c)
100
50
0
(d)
100
50
0
(e)
100
50
0
1
2
3
4
5
Per cent of alatae reared in batch
'Batch' number

produced by apterous and alate adults are given in table 37. The mean daily temperature during this experiment was 15.3°C.

If the apterous second generation adults are considered, it is found that when aphids were reared in isolation throughout the three generations only one developed as an alata. However, crowding of the third generation nymphs significantly increased alata production (χ^2=25.24, $p < 0.001$) to 67%. Crowding the second generation only also resulted in a significant increase (χ^2=75.10, $p < 0.001$) to 95%. Crowding the second and third produced as many alatae as crowding only the second (χ^2=0.09, $p > 0.05$) but more than only crowding the third (χ^2=11.04, $p < 0.001$). Only one alate was produced when the fundatrix only was crowded. The proportion of alates was increased when the first and third generations were crowded (χ^2=54.67, $p < 0.001$) and when the first and second were crowded (χ^2=46.91, $p < 0.001$). Crowding all three generations resulted in more alatae than crowding the first and third (χ^2= 5.02, $p < 0.05$) but a similar proportion to crowding the first and second (χ^2= 0.34, $p > 0.05$).

It can be seen from table 37 that alatae readily give rise to other alatae, whether they or their offspring were reared in crowded conditions. However, apart from the two instances when the second and third were crowded and when these two were isolated, apterous adults produced more alatae than did winged individuals. A summary of the statistical results of each treatment is given in table 38.

When apterous mothers which had been crowded during their development were isolated at the teneral stage, there appeared to be a change in the mother's response (fig.129), similar to that found for the fundatrices. When offspring were reared in isolation the proportion of alatae amongst them fell (fig.129a). However this decline was much less marked in cases where the rearing treatment for each generation was cr/cr/i, suggesting

Table 38 Difference in the production of alate offspring by adults of the second generation

Treatment of 1st,2nd & 3rd generation	Proportion of alates produced by adults: Apterous	Alate	χ^2	Significance
i/cr/i	95.0	47.2	26.43	$p < 0.001$
i/cr/cr	95.4	96.8	0.03	$p > 0.05$
cr/i/i	3.7	0	0.07	$p > 0.05$
cr/i/cr	88.7	68.0	6.06	$p < 0.05$
cr/cr/i	94.3	50.0	12.64	$p < 0.001$
cr/cr/cr	98.1	80.2	14.90	$p < 0.001$

Table 39 The form of the fourth generation resulting from rearing previous generations in crowded (cr) and isolated (i) conditions

Treatment and form of: Fundatrix	2nd gen.	3rd gen.	4th gen.	Ap	Al	% Al	Mortality of offspring (%)
i	cr (Ap)	i (Al)	cr	31	1	3.1	20.0
i	cr (Ap)	i (Ap)	cr	33	3	8.3	30.7
i	cr (Ap)	i (Ap)	i	17	0	0	29.2
i	cr (Ap)	cr (Ap)	cr	0	54	100.0	12.9
i	cr (Ap)	i (Al)	i	20	0	0	16.7
i	i (Ap)	i (Ap)	i	24	0	0	11.1
cr	cr (Al)	i (Al)	cr	50	2	3.8	23.5
cr	cr (Al)	i (Al)	i	21	0	0	19.2
cr	i (Al)	i (Ap)	cr	27	0	0	10.0
cr	i (Al)	cr (Ap)	i	19	0	0	20.8
cr	i (Al)	cr (Ap)	cr	3	34	91.9	28.8
cr	i (Al)	cr (Al)	cr	30	7	18.9	27.5
cr	cr (Al)	cr (Al)	cr	41	4	8.9	32.8
cr	cr (Al)	cr (Al)	i	23	0	0	17.8
cr	i (Al)	i (Ap)	i	28	0	0	3.5

Figure 129:

Proportions of alatae in successive batches of offspring produced by second generation apterous adults

(Treatments given are conditions of rearing of 1st, 2nd and 3rd generations; i = isolated, cr = crowded)

Mother reared crowded, isolated at teneral stage:

(a) i/cr/i

(b) cr/cr/i

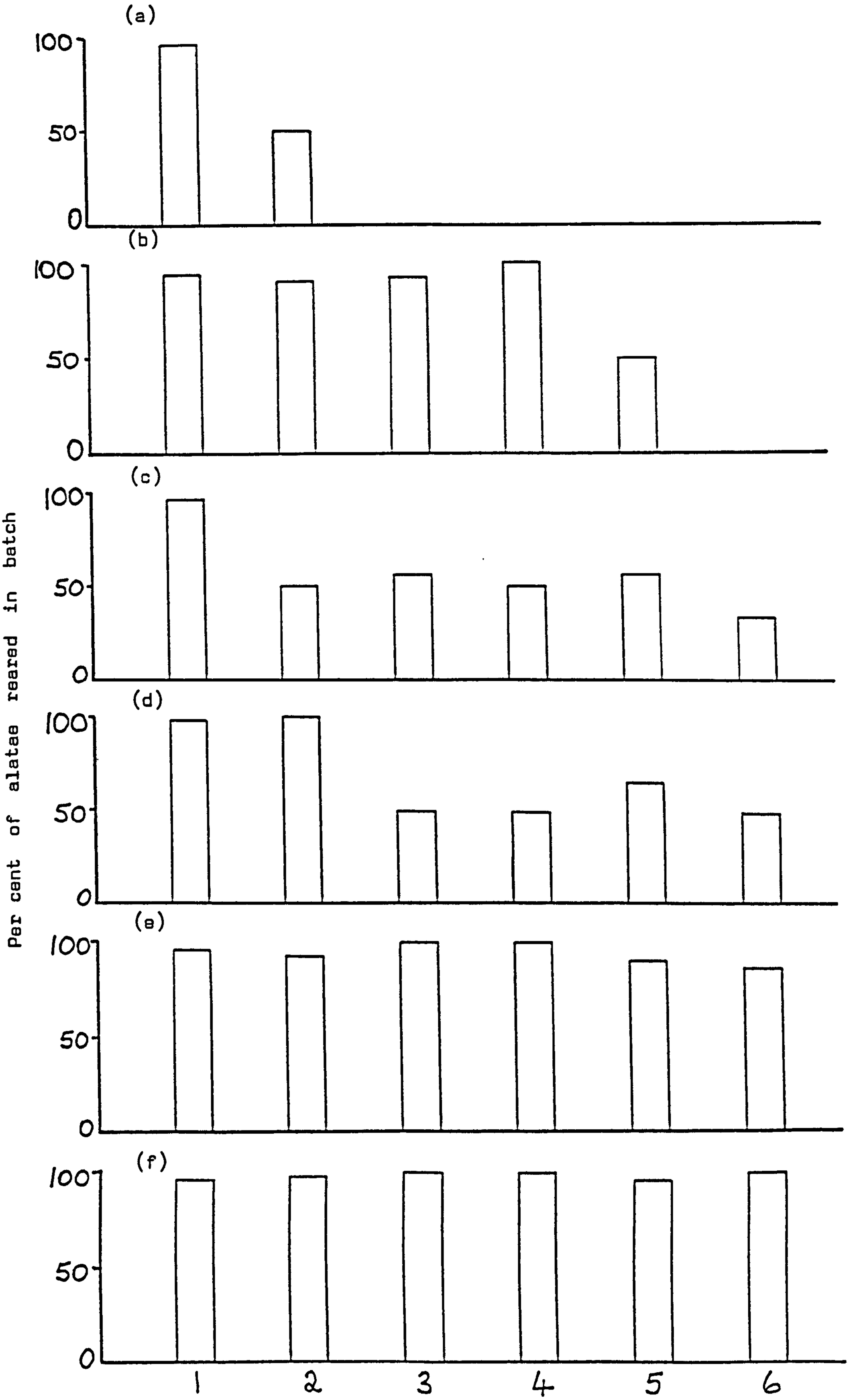
(c) i/cr/cr

(d) cr/cr/cr

Mother crowded throughout life:

(e) cr/cr/i

(f) cr/cr/cr


(a)
100
50
0
(b)
100
50
0
(c)
100
50
0
(d)
Per cent of alatae reared in batch
100
50
0
(e)
100
50
0
(f)
1
2
3
4
5
6
'Batch' number

that the conditions in which the fundatrix were reared had an influence upon the form of the third generation. Although there was no difference in the proportion of alates produced in the first batch of offspring ($\chi^2 = 0.02$, $p > 0.05$), there was in the second ($\chi^2 = 8.56$, $p < 0.01$). By the third, offspring from the i/cr/i treatment were all apterous, whereas 92% were alatae from the cr/cr/i treatment. By the fifth batch this figure was 50% and all of the sixth and last batch from cr/cr/i were apterous (fig.129b).

Offspring from i/cr/cr showed a decline in alatae produced after the first week but thereafter the proportion levelled out, indicating that the nymphal response did not change considerably over the mother's reproductive life (fig.129c). Offspring from cr/cr/cr showed in general a higher proportion of alatae than those from i/cr/cr, again suggesting the influence of the fundatrix on the third generation (fig.129d). Offspring reared from mothers which were kept crowded throughout their lives produced similar proportions of alatae throughout (fig.129,e,f). Thus it seems likely that the waning of the mother's response to crowding was caused by their isolation at the teneral stage.

When alate mothers were isolated at the teneral stage, proportions of alatae in successive batches of offspring fell (fig.130). There were no differences in the alatae produced between i/cr/i and cr/cr/i in the first or second batch ($\chi^2 = 0.06$, $p > 0,05$ and $\chi^2 = 1.71$, $p > 0.05$) and by the third batch all offspring were apterous (fig.130 a,b). Offspring from cr/cr/cr produced lower proportions of alatae than i/cr/cr (fig.130c,d) suggesting that the influence of the fundatrix upon the third generation was less marked when the second generation were alate. The fact that i/cr/cr produced a substantial proportion of alatae throughout (fig.130,c) indicated that the nymphal response varied little throughout the reproductive life of the mother. Mothers which were not isolated at the

Figure 130:

Proportions of alatae in successive batches of offspring produced by second generation alate adults.
(Treatments are conditions of rearing of 1st, 2nd and 3rd generations; i = isolated, cr = crowded).

Mother reared crowded, isolated at teneral stage:

(a) i/cr/i

(b) cr/cr/i

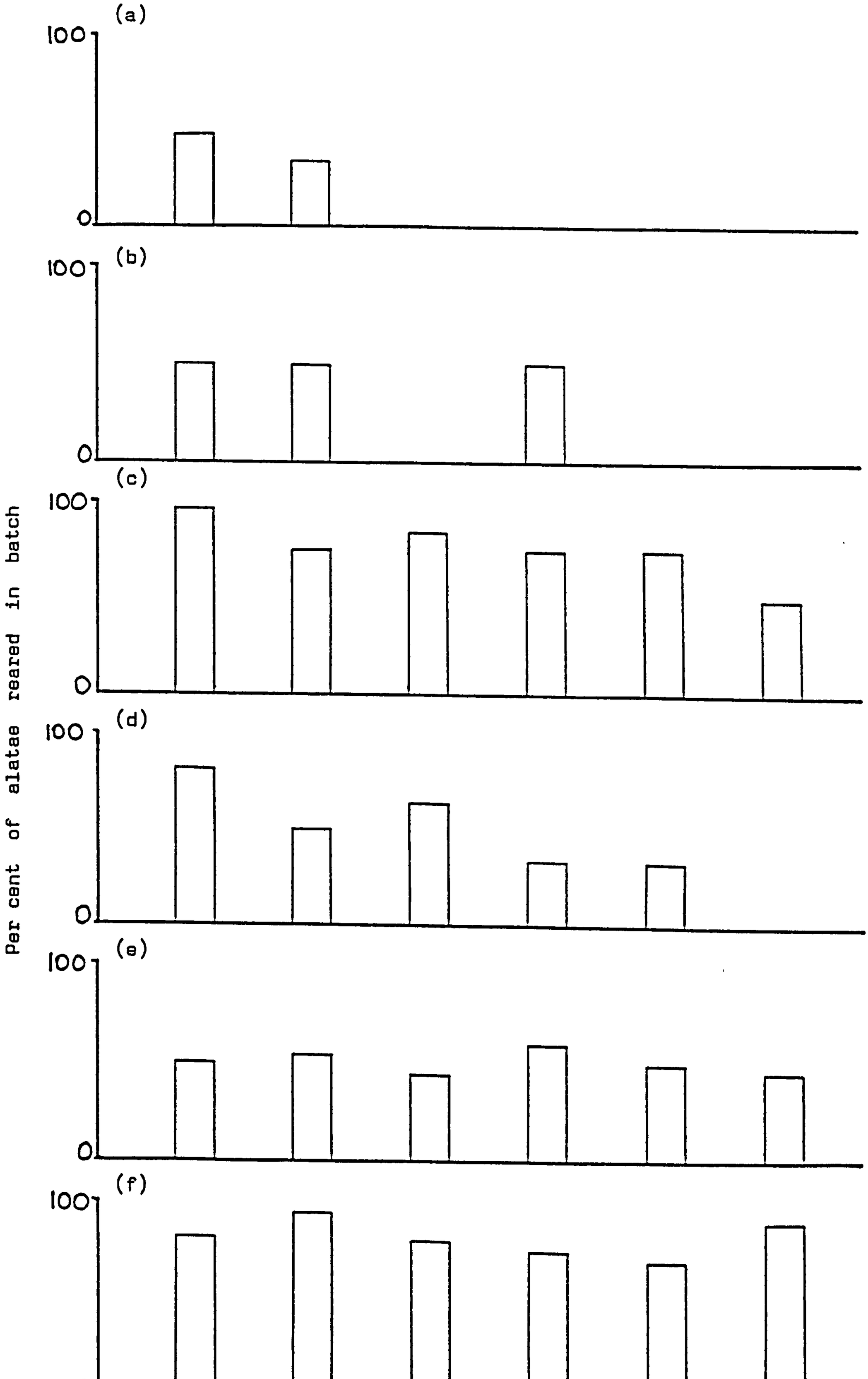
(c) i/cr/cr

(d) cr/cr/cr

Mother crowded throughout life:

(e) cr/cr/i

(f) cr/cr/cr


(a)
100
0
(b)
100
0
(c)
100
0
(d)
100
0
(e)
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(f)
100
0
1
2
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5
6
'Batch' number
Per cent of alatae reared in batch

teneral stage continued to produce similar quantities of alatae throughout (fig.130 e,f) indicating that the change in the mother's response was due to its isolation.

Certain of the offspring from the above treatments were reared crowded and in isolation. The forms taken by these adults of the fourth generation are given in table 39. The mean daily temperature during the experiment was 17.7°C.

Few alatae were produced from alate mothers of the third generation but this inhibition did not result from alate mothers of the second generation. Large numbers of alatae were produced when third and fourth generations were crowded and the third generation were apterous. The restraining influence on alatae of alata production thus appeared to operate in this generation. Alata production was again determined pre- and postnatally with highest proportions being produced when mother and offspring were crowded.

The forms taken by the fifth generation are given in table 40. The mean daily temperature was 15.9°C.

The inhibition of alata production by alatae again appeared to exist, from the fourth to the fifth generation. However, this inhibition appeared not to exist after two generations, a similar finding to alata production in the fourth generation (table 39). Alata production was again determined pre- and postnatally with the highest proportion produced when both mother and offspring were crowded.

Alatae were produced in the sixth generation but only when crowded and from apterous adults which had been crowded.

Table 40 Forms of the fifth generation resulting from various rearing conditions of previous generations

Treatment and form of:								Mortality of offspring (%)
Fundatrix	2nd gen.	3rd gen.	4th gen.	5th gen.	Ap	Al	% Al	
i	i (Ap)	i (Ap)	i (Ap)	i	25	0	0	19.3
i	cr (Ap)	i (Ap)	i (Ap)	cr	24	0	0	17.2
i	cr (Ap)	i (Ap)	cr (Ap)	cr	18	12	40.0	28.6
i	cr (Ap)	i (Al)	i (Ap)	cr	20	20	50.0	20.0
cr	i (Al)	i (Ap)	cr (Ap)	cr	16	42	72.4	28.4
cr	i (Al)	i (Ap)	i (Ap)	cr	20	31	60.8	26.5
cr	cr (Al)	cr (Al)	cr (Al)	cr	45	3	6.2	21.3

The first three generations were reared in crowded and isolated conditions on alder saplings, at two constant temperatures, 10°C and 20°C. The form of the second generation at 10°C is given in table 41a and that of the third in table 41 b. Only the first batch of offspring was considered.

The same trends emerge from table 41 as occurred in the field. Crowding the second generation nymphs increases alata production significantly (χ^2= 7.99, p<0.01) as does crowding the fundatrix (χ^2= 8.93, p< 0.01). Crowding both results in an even higher proportion (χ^2 = 48.17, p< 0.001). There were no differences between any of the proportions of alates produced in the third generation (table 41) and those produced by the corresponding treatments in the field. A summary of the statistical results is given in table 42.

The form of the second generation at 20°C is given in table 43a and that of the third in table 43b. None of these proportions were different from those at 10°C , and only the cr/i treatment was different from that in the field (χ^2= 5.30, p<0.01).

There were differences between the proportion of alatae produced at 20°C and at 10°C. A summary of the statistical results is given in table 44. Alata production appeared to be reduced at 20°C, this occurring both pre- and postnatally. In contrast to the results at 10°C (table 42) there were differences between the proportions of alatae produced at 20°C and in the field (table 45). Alata production was reduced at 20°C compared to field conditions where the average temperature was 15°C.

Table 41a The effect of exposing mothers and offspring to crowded (cr) and isolated (i) conditions on the form of the 2nd gen. at 10°C

Fundatrix	Offspring	Ap	Al	%Al	Mortality of offspring
i	i	18	0	0	10.0
i	cr	26	17	39.5	10.8
cr	i	13	11	45.8	20.0
cr	cr	1	38	97.4	9.3

Table 41b The form of the third generation at 10°C (only apterous second generation used).

Fundatrix	2nd gen.	3rd gen.	Ap	Al	%Al	Mortality of offspring
i	i	i	16	0	0	20.0
i	i	cr	13	17	56.7	16.7
i	cr	i	3	18	85.7	16.0
i	cr	cr	1	28	96.6	12.1
cr	i	i	17	0	0	15.0
cr	i	cr	6	17	73.9	40.9
cr	cr	i	3	21	87.5	7.7
cr	cr	cr	2	32	94.2	22.7

Table 42: Comparison between alata production in the third generation: 10°C and field (average temperature 15.3°C).

Treatment	% Al field	% Al 10°C	χ^2	Significance
i/i/i	2.8	0	0.16	$p > 0.05$
i/i/cr	66.7	56.7	0.22	$p > 0.05$
i/cr/i	95.0	85.7	0.84	$p > 0.05$
i/cr/cr	95.4	96.6	0.09	$p > 0.05$
cr/i/i	3.7	0	0.06	$p > 0.05$
cr/i/cr	88.7	73.9	1.81	$p > 0.05$
cr/cr/i	94.3	87.5	0.08	$p > 0.05$
cr/cr/cr	98.1	94.2	0.20	$p > 0.05$

Table 43 a The effect of exposing mothers and offspring to crowded (cr) and isolated (i) conditions on the form of the 2nd gen.at 20°C.

Fundatrix	Offspring	Ap	Al	% Al	Mortality of offspring (%)
i	i	18	0	0	10.0
i	cr	32	28	46.7	21.1
cr	i	14	3	17.6	15.0
cr	cr	8	51	86.4	25.3

Table 43 b The form of the third generation at 20°C (only apterous second generation used)

Fundatrix	2nd gen	3rd gen	Ap	Al	% Al	Mortality of offspring (%)
i	i	i	22	0	0	15.4
i	i	cr	21	12	36.4	17.5
i	cr	i	24	1	4.0	7.7
i	cr	cr	21	21	50.0	14.3
cr	i	i	19	0	0	5.0
cr	i	cr	36	6	14.3	19.2
cr	cr	i	16	1	5.8	20.0
cr	cr	cr	12	26	68.4	15.6

Table 44 Comparison between alata production in the third generation at 20°C and 10°C

Treatment	% Al 10°C	% Al 20°C	χ^2	Significance
i/i/i	0	0		
i/i/cr	56.7	36.4	3.49	$p > 0.05$
i/cr/i	85.7	4.0	34.89	$p < 0.001$
i/cr/cr	96.6	50.0	19.63	$p < 0.001$
cr/i/i	0	0		
cr/i/cr	73.9	14.3	25.79	$p < 0.001$
cr/cr/i	87.5	5.8	30.04	$p < 0.001$
cr/cr/cr	94.2	68.4	7.78	$p < 0.01$

Table 45 Comparison between alata production in the third generation: 20°C and field (average temperature 15.3°C).

Treatment	% Al field	% Al 20°C	χ^2	Significance
i/i/i	2.8	0	0.06	$p > 0.05$
i/i/cr	66.7	36.4	3.96	$p < 0.05$
i/cr/i	95.0	4.0	63.29	$p < 0.001$
i/cr/cr	95.4	50.0	28.11	$p < 0.001$
cr/i/i	3.7	0	0.03	$p > 0.05$
cr/i/cr	88.7	14.3	54.16	$p < 0.001$
cr/cr/i	94.3	5.8	35.70	$p < 0.001$
cr/cr/cr	98.1	68.4	24.56	$p < 0.001$

3.2. DISCUSSION

The fundatrix of P.alni is apterous and crowding nymphs from egg hatch did not result in any alate individuals. In certain members of the family Callaphididae the fundatrix possesses wings and successive generations of virginoparae are also winged. In most aphids, apterous fundatrices give rise to generations which may be apterous or alate (Hille Ris Lambers, 1966) and this appears to be the case for P.alni.

The fundatrix responds to crowding during its development by producing alate offspring. The nymphs are also responsive and greatest proportions of alatae are produced in the second generation when both mother and offspring are crowded. Similar responses to crowding were observed in A.craccivora (Johnson, 1965), A.fabae (Shaw 1970a), R.padi (Dixon and Glen, 1971), R.insertum (Dewar, 1976) and S.avenae (Watt and Dixon, 1981). No alatae were produced in the second generation when both fundatrix and offspring were reared in isolation. More alatae developed when only the fundatrix was crowded compared to crowding the offspring. This suggests that the prenatal effect has a greater influence upon alata production than the postnatal. This is further evidenced by the graphs of fig.127, whereby crowding the offspring results in a relationship between intensity of crowding and alata production but only when the fundatrix is reared in isolation. It is likely that when the fundatrix is reared in crowded conditions the prenatal effect precludes any relationship.

When the crowding stimulus to the mother is removed, by isolation at the teneral stage, the response of the mother also changes. The response to crowding by the nymphs remains similar but the mother begins to exert less influence on the production of alatae and successive batches of offspring, reared in isolation, produce less alatae (fig.128). This changing of the mother's response is similar to that reported for M.viciae (Lees, 1967)

in which mothers tended to produce less alatae with time after a crowding stimulus. This changing of response would be advantageous to the aphid if environmental conditions suddenly changed. An example of this is the spraying of LF125 in 1982. The original population density was high and alatae were being produced at the time of spraying. When the majority of aphids were removed, the population became sparse and so in order to build up the numbers again it would be an advantage to produce apterous individuals, rather than the less fecund alatae. A similar situation exists when populations peak and crash naturally and very few aphids remain.

The form of the third generation appears to be controlled by similar responses in mothers and offspring crowding as that of the second generation. However, when the adults of the second generation are alate, the production of winged individuals is suppressed (table 38). A similar suppression was noted for T.maculata (Toba et al, 1967) and M.dirhodum (Elkhider,1979). In some aphids alatae are thought never to produce alatae (M.viciae, Lees 1966; A.pisum, Sutherland, 1970). However, Burns (1972) found that in M.viciae alatae which had flown produced few if any alatae whereas those which had not, produced alatae as readily as did apterae. The production of alatae after flight was not tested in P.alni but if a similar situation occurs in this aphid it might help to explain the relatively large proportions of alatae produced by alatae (table 37).

The intrinsic mechanism of alata suppression was termed the 'interval timer' by Lees (1960). A similar influence on succeeding generations by the fundatrix has also been reported; this was termed the 'facteur fondatrice' by Bonnemaison (1951). In this case the influence is the suppression of sexual forms in spring. In P.alni the fundatrix also appears to have an influence on the reactions of her grand-daughters. In this case, crowding of the fundatrix and the second generation resulted

in less of a decline in the production of apterae in the third generation (fig.129). The influence of crowding on the fundatrix was passed on to her daughter and this influence was sustained longer than if the daughter only was crowded. This effect only occurred, however, when the second generation adult was apterous. This again suggests that the production of alatae is not so strong in the alatae themselves.

The suppression was notable in the fourth and fifth generations. However, it appears from these results (tables 39 and 40) that the suppressive influence does not take effect over two generations. A clear indication of this is given by the three treatments, with form of the adults in brackets:

A: cr/i (Al)/cr (Ap)/cr

B: cr/i(Al)/cr(Al)cr

C: cr/cr(Al)/cr(Al)/cr

Treatment A produced 92% alatae, B,19% and C, 9%. Thus it appears that the alate adults in the third generation in B were suppressed in their alata production, compared to the apterous adults in A. When all generations were crowded and the second and third alate, production was suppressed still further. An 'interval timing' system thus operates in the production of alatae in P.alni. This timer wanes with the passage of time such that after two generations it has little effect. The fact that some alate individuals responded to crowding like apterae indicates that the timer is 'weak' in this aphid, similar to A.craccivora (Johnson and Birks,1960) as opposed to a 'strong'influence such as with M.viciae (Lees,1967).

High temperatures have been shown to have a suppressive influence upon alata production in several aphid species. C.fragaefolii is an aphid in which alata production is controlled almost exclusively postnatally (Judge and Schaefers, 1971). An increase in temperature from 15.6°C to 23.9°C

significantly reduced alata production, but this effect was found to be wholly prenatal (Schaefers and Judge,1971). A similar increase in temperature from 15°C to 23°C was found to suppress alate production prenatally in M.viciae, an aphid in which crowding also acts prenatally (Lees,1967). Johnson (1966b) found that high temperatures suppressed alata production postnatally in A.craccivora, an aphid in which crowding acts pre- and postnatally (Johnson,1965). In P.alni a change in temperature from 10°C to 20°C appears to suppress alata production at the pre- and postnatal levels (table 44). This action appeared to have a greater effect upon the mother, rather than on the nymphs. The significance of the suppression varied when nymphs were crowded, but was highly significant when the mother was treated thus. The 'shock' of high temperature has been suggested to act upon the embryo itself (Lees,1967). This was also suggested by Schaefers and Judge (1971) who thought that temperature affected all but the most mature embryos, as alata production was suppressed within one day of transfer from 15°C to 24°C.

In the past the interaction between crowding and host plant influences has led to many problems in interpretation of data. Firm evidence of the role of the host plant has been provided by Johnson (1966a), Sutherland (1969b), Dixon and Glen (1971) and Watt and Dixon (1981). In these studies, alata production was increased on mature or senescing tissue. It has been suggested that on mature leaves aphids are more restless (Johnson and Birks,1960; Lees,1967) thus leading to an increased frequency of alata-inducing interactions. The host plant does not appear to play an important role in alata production in P.alni. Alatae appear at different times of the year, according to population density. In S.avenae (Watt and Dixon,1981) at the same aphid density there was a higher proportion of presumptive alatae on old growth stages of wheat than on early stages. This does not occur with P.alni. Individuals if reared in isolation throughout the season on the windbreak are all

apterous. A similar situation occurs with R.padi (Dixon and Glen,1971) but only if the leaf tissue is actively growing. Alatae generally occur when the soluble nitrogen content of the alder leaves is falling (chapter 5). However, under constant conditions, in a temperature room where food quality may be assumed to be relatively stable, alates are produced in similar quantities to the field (table 42).

Throughout these experiments much variability in reactions was noted not only between aphids but also within the progeny of one mother. Such variability has been noted by other workers (Lees,1967; Burns,1972; Elkhider,1979). Variability may be due to small variations in age or development rate of aphids. Although it has been stated that the host plant does not appear to affect alata production in P.alni, variations in individual leaf quality may be a factor. It is likely that the amount of stimulation each aphid receives in crowding is the main reason for the variation. Alata production can result from tactile stimulation (Lees, 1966). Such stimulation is presumed to act on the developing embryos through the endocrine system of the mother (Bonnemaison,1951). Kennedy and Stroyan (1959) were among the first authors to suggest that the endocrine system and in particular the corpus allatum (CA) may control early determination and the subsequent development of apterous aphids. Hales (1976) suggested that conditions such as isolation might induce a high level of juvenile hormone in reproductive aphids thus inhibiting the development of their embryos as alatae. Under this maternal influence the CA of 'apterized' embryos would also be present at a high level of activity for subsequent development. In aphids where alata determination is postnatal (e.g.C.fragaefolii, Judge and Schaefers,1971) apterizing conditions would directly influence CA activity in the new born nymphs. Leckstein and Llewellyn (1975) could find no evidence that the maternal CA is involved in the prenatal control of alary polymorphism in M.viciae, however and Lees (1977) reported that the control of wing polymorphism

whether in the parent (M.viciae) or the embryo (A.fabae) was not mediated by juvenile hormone. More recently, Mackauer, Nair and Unnithan (1979) reported that precocene II, a compound with anti-JH activity (Bowers, Ohta, Cleere and Marsella, 1976) induced alata production in isolated apterae of A.pisum. The effect could be reversed with JH 1. Delisle, Cloutier and McNeil (1983) concluded that precocene II induces alata production in M.euphorbiae when kept in conditions which could otherwise produce apterae. These authors concluded that JH is involved in the prenatal determination of the apterous morph in that aphid and that the action of the precocene is to inactivate the CA. As stated by Cloutier (1984), the mechanism is still poorly understood but it seems quite clear that the production of alatae is under hormonal control. If this is so it may explain some of the variation noted in alata production; the inability of all embryos to become alatae may be due to differing sensitivity of the embryos to the hormone or different exposure to it within the mother. Such a reason for variation was proposed by Dewar (1976) working with alata production in R.insertum.

3.3. FLIGHT IN P.ALNI

3.3.1. Introduction

Locomotory activity in animals has been classified as 'migratory' or 'trivial' (Kennedy 1961; Southwood 1962). Migratory movements occur when the thresholds for stimuli such as a mate or food are high and result in an animal leaving its habitat. Trivial movements occur when these thresholds are lower and result in the redistribution of an animal within its habitat. Such activity was defined for the sycamore aphid (Dixon, 1969) with both migratory and trivial flight involved. It was originally thought that all alate aphids were obligate fliers (Johnson,1960; Kennedy, 1961; Southwood 1962). It has since been shown that flight activity in

aphids may be influenced by past or present experiences. In M.viciae the degree of crowding at the time of the adult moult influences the proportion of alatae which fly (Dixon, Burns and Wangboonkong,1968). M.viciae is an aphid in which alata production is controlled prenatally (Lees, 1967) but in D.platanoidis, all viviparae of which are alate, a similar effect occurs (Dixon 1969), flight depending on the current experience of crowding and nutrition. Crowding during nymphal and parental lives affects alata production and influences flight in A.fabae (Shaw, 1970 a,b). Flight in E.tiliae is also influenced by present and previous generations' experience of crowding (Kidd,1977), as well as changes in the leaves induced as a result of aphid feeding. Migration in polyphagous aphids as a result of the host plant becoming unsuitable has been reported for S.avenae (Watt and Dixon,1981).

The aim of this section has been to examine the effect of crowding on flight in P.alni and some of the physiological changes which the aphid undergoes before and after flight. The seasonal flight pattern observed in the field at East Malling and on a national scale, using suction trap data from the Rothamsted Insect Survey is discussed and related to changes in population abundance.

3.3.2. Laboratory experiments

Alate adults of the second generation were used in all experiments. These were reared in crowded and isolated conditions as described in section 3.1.2. Soon after moulting to adults but before the wings were properly hardened they were transferred to small A.glutinosa saplings. Each sapling bore ten leaves, the petioles of which were banded in 'Oecotak'. Saplings were placed in flight cabinets, built to the design described by Dixon (1969) and illustrated in fig.131. Four treatments were examined by: (a) rearing aphids in isolation and placing one on

Figure 131:

Flight cabinet: Chamber A is painted matt black and separated by a non-return arrangement of glass from Chamber B which is white.

Figure 132:

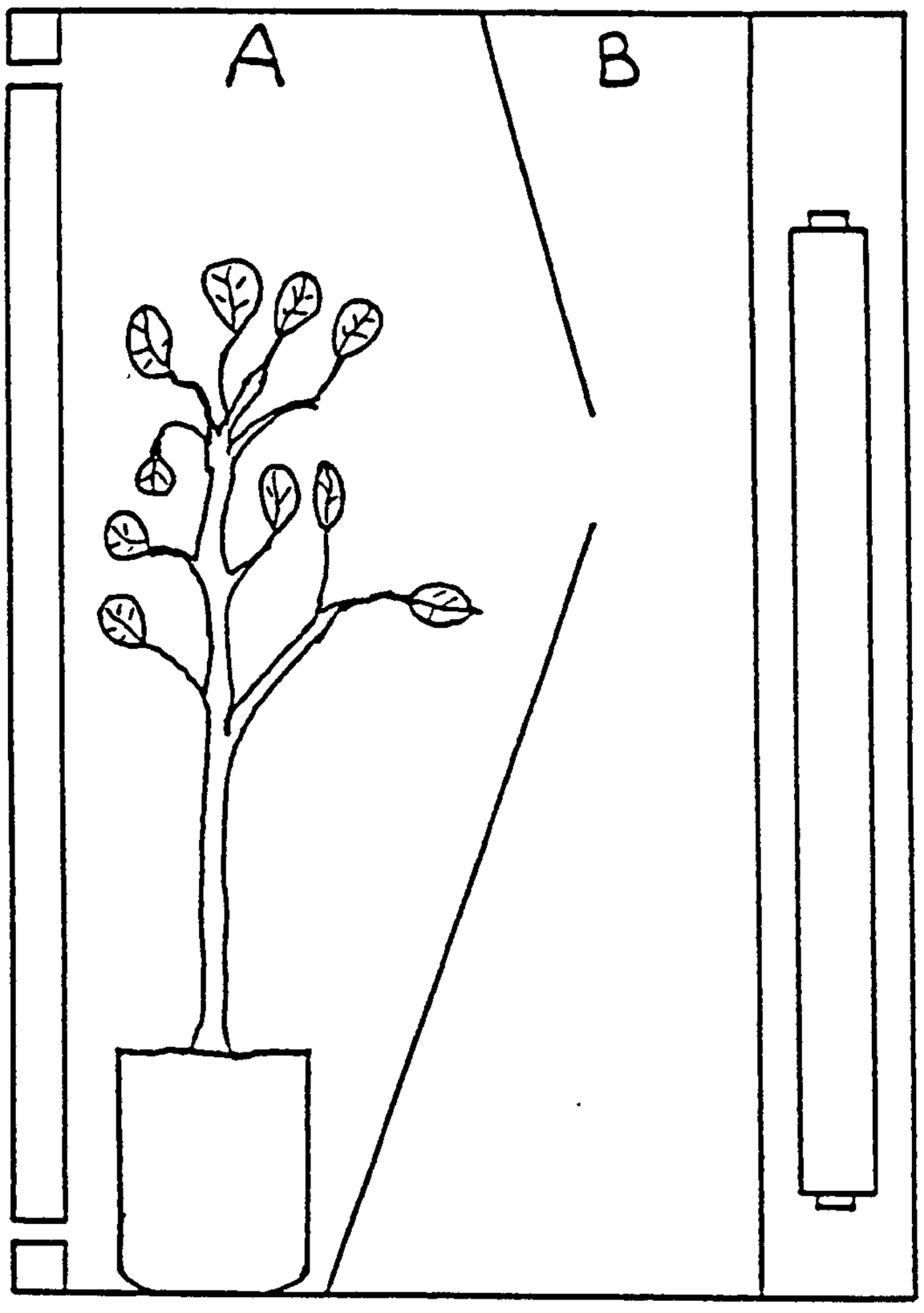
Arrangement of saplings in greenhouse to examine settling of P.alni

g = A.glutinosa

c = A.cordata

i = A.incana

◀ - release point of alatae



g c i ◀

i g c ◀

c i g ◀

c i g ◀

g c i ◀

i g c ◀

i g c ◀

c i g ◀

g c i ◀

2m

a leaf; (b) rearing in isolation and placing ten on each leaf; (c) rearing crowded, placed one on a leaf and (d) rearing crowded, placed ten on a leaf. Experiments were examined daily and the number of aphids flying in the previous 24 hr. recorded. The experiment was continued for seven days and repeated three times. It was attempted to mark individual aphids which had flown with quick drying paint. Returning these to the flight chamber would thus keep the population density stable and also provide a way of recording how many aphids made more than one flight. However, the small size (average teneral weight,0.112 mg) of the alates made this impractical. Aphids which had flown were therefore not returned to the flight chamber. Any nymphs produced by the alates remaining upon the tree were counted and removed daily. The number of aphids responding with flight after 24 hours in the various treatments is given in table 46.

When the alatae were isolated at adulthood, there was no difference in the proportion flying from those that had been reared crowded or isolated (Av.C : $\chi^2 = 1.57$, $p > 0.05$). However, when the alatae were crowded at adulthood, a greatly increased proportion flew, regardless of whether they were reared singly (AvB: $\chi^2 = 49.16$, $p < 0.001$) or crowded (CvD: $\chi^2 = 44.45$, $p < 0.001$). Thus it appears that if alatae of P.alni are to migrate, they need the stimulus of crowding when they become adult.

The daily flight under each treatment is given in table 47. It can be seen that when crowded most of the alatae which flew did so in the first day. When isolated, alatae continued to commence flight for longer periods.

By the second day, flight activity was not significantly different between crowded and isolated alatae (AvB: $\chi^2 = 1.23$, $p > 0.05$ and CvD: $\chi^2 = 0.09$, $p > 0.05$). Flight activity in the first day of adult life is

Table 46: The number of aphids responding by flight in different rearing and adult conditions.

Nymphal experience	Experience in cabinet after adult moult	Total number of aphids which flew	did not fly	% flyers
A: isolated	isolated	5	25	16.7
B: isolated	crowded	228	72	76.0
C: crowded	isolated	8	22	26.7
D: crowded	crowded	240	60	80.0

Table 47: Flight activity of P.alni in crowded and isolated conditions.

	A: i/i		B: i/cr		C: cr/i		D: cr/cr	
Day	No.of aphids	No. flying	No.of aphids	No. flying	No.of aphids	No. flying	No.of aphids	No. flying
first	30	5	300	228	30	8	300	240
second	25	3	72	21	22	2	60	6
third	22	2	51	6	20	1	54	6
fourth	20	1	45	0	19	1	48	0
fifth	19	1	45	0	18	1	48	0
sixth	18	0	45	0	17	0	48	0
seventh	18	0	45	0	17	0	48	0

thus greatly increased when the alatae are crowded. Of all the aphids that flew, the proportion flying on day 1 of each treatment is given in table 48.

Because the petioles of the leaves upon which the aphids were placed were banded with 'Oecotak' it was possible to monitor, by assigning each leaf a number, whether when the alatae were isolated they gave birth before flying. No nymphs were found upon the leaves in the cabinets containing crowded aphids until day 4, and as the last alata flew on day 3 it is obvious that in crowded conditions, no nymphs were deposited before flying. The full results are given in table 49.

It can be seen that alata becoming adult in conditions of low population density, simulated by one adult per leaf, are more likely to deposit nymphs before flying than those which become adult in crowded conditions.

A sample of thirty alatae were taken within twelve hours of the adult moult, weighed and dissected. The mean weight of these aphids was 0.112 mg. $\pm$ 0.004 mg. All aphids were found to contain small embryos, but none of these possessed pigmented eyes. There was a significant relationship between the weight at maturity and the number of embryos the aphid contained ($r = 0.895$, d.f. $=28$, $p < 0.001$) (fig.133). After flight in the cabinets alatae were caged individually on A.glutinosa leaves outside. Samples of thirty were taken after 4,7,14,21 and 28 days. The number of offspring produced in that time, weight and number of embryos with pigmented eyes were recorded. The potential reproductive capacity of the aphids was expressed as embryos per mg. of aphid. The results are presented in fig.134a-d.

Soon after flight, alatae matured embryos and began reproduction. Their weight increased such that after four days this was 1.5 times that at

Table 48: Of all the aphids that flew, the proportion flying on day 1.

Treatment		% of fliers that
nymph	alata	flew on day 1
i	i	41.7
i	cr	85.7
cr	i	61.5
cr	cr	95.2

Table 49: The number of nymphs deposited before flying by alata in crowded (cr) and isolated (i) conditions.

Nymphal experience	alata experience	No.of aphids flying	No.of nymphs deposited before flight
i	i	12	19
i	cr	228	0
cr	i	13	25
cr	cr	240	0

Figure 133:

The relationship between the weight of an alata of P.alni and the total embryo content shortly after moulting to maturity.

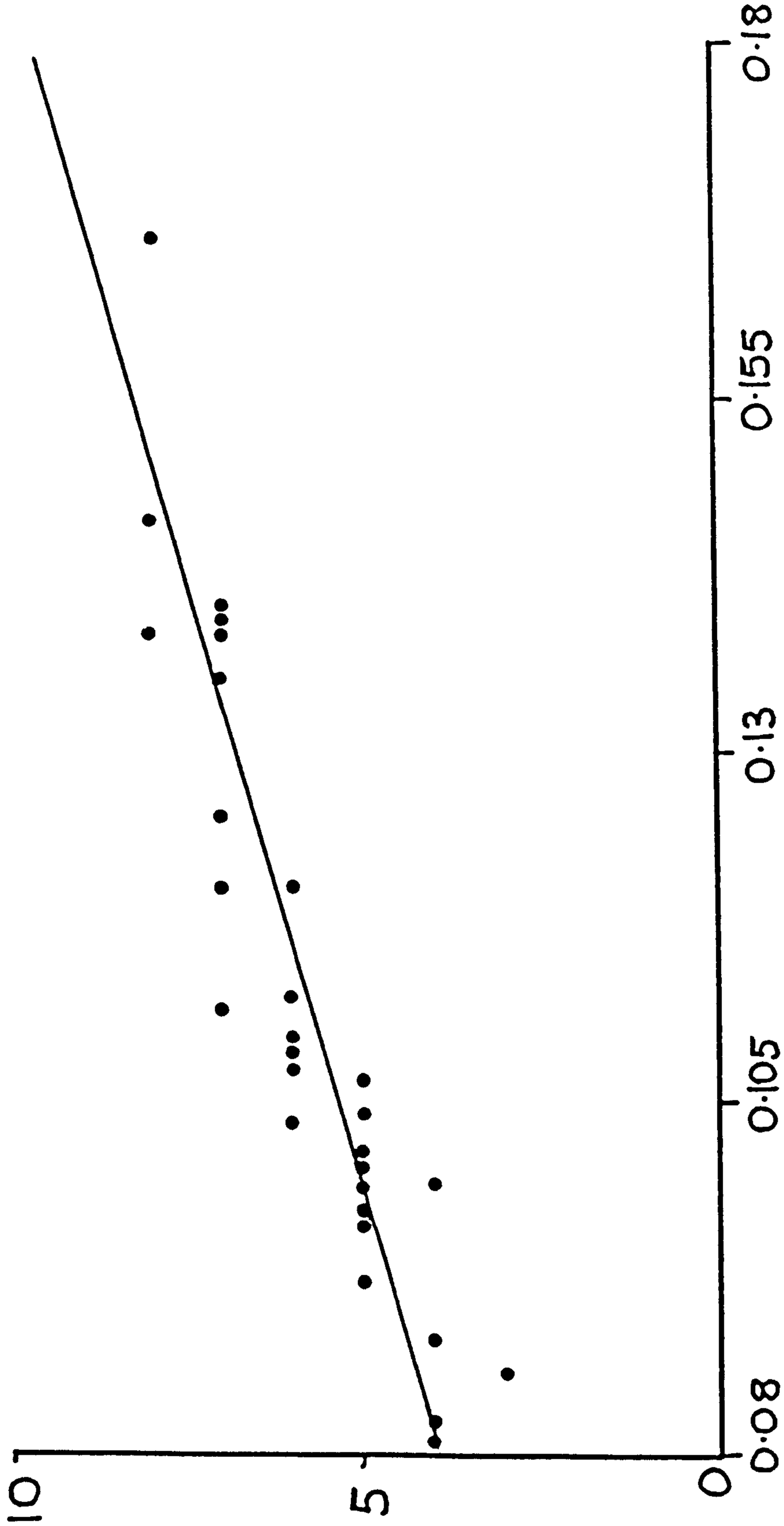

0·18
0·155
0·13
0·105
0·08
0
5
10
weight of alata / mg
total embryo content

Figure 134:

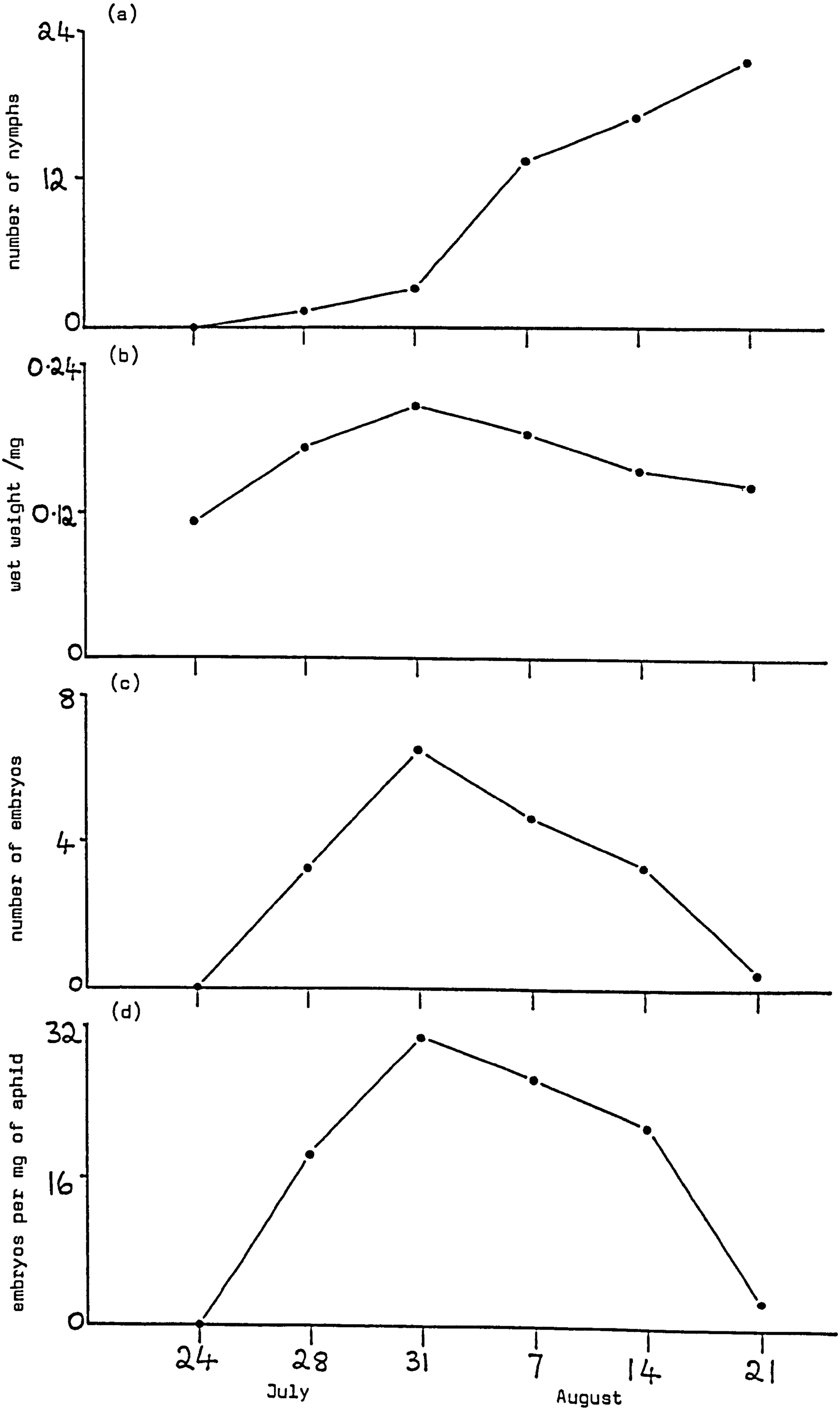
Changes in alata physiology after moulting to adulthood

(a) Cumulative number of nymphs produced

(b) Wet weight

(c) Number of embryos with pigmented eyes

(d) Embryos per unit weight of aphid


(a)
24
12
0
number of nymphs
(b)
0·24
0·12
0
wet weight /mg
(c)
8
4
0
number of embryos
(d)
32
16
0
embryos per mg of aphid
24
28
31
7
14
21
July
August

maturity (d=7.7, $p<0.001$) and after a week, 1.9 times (d=10.2, $p<0.001$); highly significant increases. Reproductive capacity reached a peak at this time and both this and weight fell subsequently.

Fourth instars (presumptive alatae) were collected from a windbreak at East Malling, where conditions were very crowded. These were placed in a plastic box and all alatae produced within twelve hours taken, to examine the settling responses of P.alni. Small aphid-free saplings of A.glutinosa, A.incana and A.cordata each about 0.5m high were placed in a latin square arrangement on a greenhouse bench. The glass of the greenhouse was whitewashed and skylights were opened and covered with fine black netting. Alatae were placed in plastic boxes attached to the back wall of the greenhouse at a similar level to the top of the saplings and 2m. distant (fig.132). A maximum and minimum thermometer placed between the saplings recorded the temperature. Aphids were released at 08.00 hours and the number on each of the saplings was recorded 24 hours later. The experiment was repeated three times. The mean temperature throughout the experiment was $24^{o}C$ with a range from $16^{o}C$ to $32^{o}C$. A total of 845 alates were released. Of these 117 were found upon the alder saplings 24 hours later, a proportion of 13.8%. Of the aphids which alighted, 61.5% were on A.glutinosa, 19.6% upon A.incana and 18.9% upon A.cordata. This difference was significant ($\chi^2 = 41.89$, $p<0.001$) and thus more alatae were found settled upon A.glutinosa. Whether alatae settled preferentially upon A.glutinosa or that settling was equal and that they took off again from A.incana and A.cordata was tested by leaving one batch of trees for a further 24 hours and then re-examining them. After 24 hours, 69.8% of alatae were on A.glutinosa, 13.2% on A.incana and 16.9% on A.cordata. After a further 24 hours the proportion of alatae present on each species were, respectively, 78%, 8.0% and 14.0%. although there is some suggestion that alatae left A.incana and A.cordata none of these values were significantly different (A.glutinosa, d=0.94,

$p > 0.05$; A.incana, $d = 0.85$, $p > 0.05$; A.cordata, $d = 0.42$, $p > 0.05$). 6% of the alatae present after 24 hours had disappeared after 48 hours indicating that some aphids had taken off again and had thus flown more than once.

3.3.3. Field studies

Sticky traps consisting of plastic cylinders, 20cm in diameter by 30cm long were positioned 1.5m above the ground at East Malling (fig.1). Traps were placed at the orchard edge, 5m from the windbreak (WM110) and in the orchard, 20m distant. Traps were also placed within the canopy, at 3.5m and 7.5m (two at each height). Three traps were placed midway between LF125 and LF126 (fig.1). A sheet of 'superglaze' (Transatlantic Plastics Ltd., Weybridge) coated with 'Oecotak' was clipped around each cylinder. Traps were examined weekly. The number of alate and non alate P.alni were counted and a fresh piece of superglaze and 'Oecotak' was then applied. Suction trap data for Wye and Silwood Park, the nearest two localities to East Malling and Lyne, were obtained by kind permission of the Rothamsted Insect Survey.

Aphids caught on the sticky traps at the orchard edge are regarded as migrating. The weekly trap catches illustrated in figs.135-137 indicate that there is one main period of flight activity per year. In all cases, the peaks of frequency of migratory flight were preceded by peaks in abundance of fourth instars (presumptive alatae) on the section of windbreak opposite the traps. A sharp decline in the numbers of these fourth instar aphids coincided with the peak in flight activity. This finding suggests that individuals were undertaking migratory flight soon after moulting to the adult stage, supporting the results of the laboratory experiments, reported earlier (table 47). On occasions when population density on the windbreak was high, migratory flight was also greater.

Figure 135:

Production and migration of alatae, LF 125

(a) Alatae recorded per trap, 1983

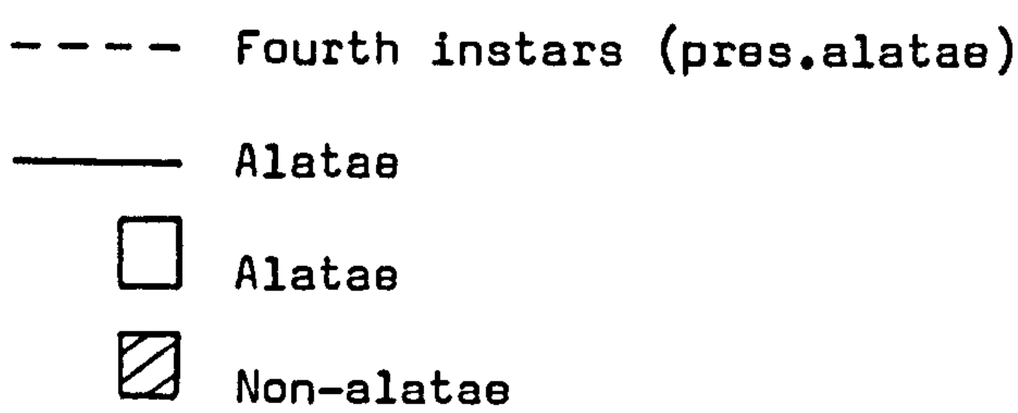
(b) Numbers of fourth instars (presumptive alatae)
and alatae on windbreak, 1983

(c) Alatae per trap, opposite section 1,1983

(d) Numbers of fourths and alatae on section 1, 1984

(e) Alatae per trap, section 2, 1984

(f) Fourths and alatae on section 2, 1984



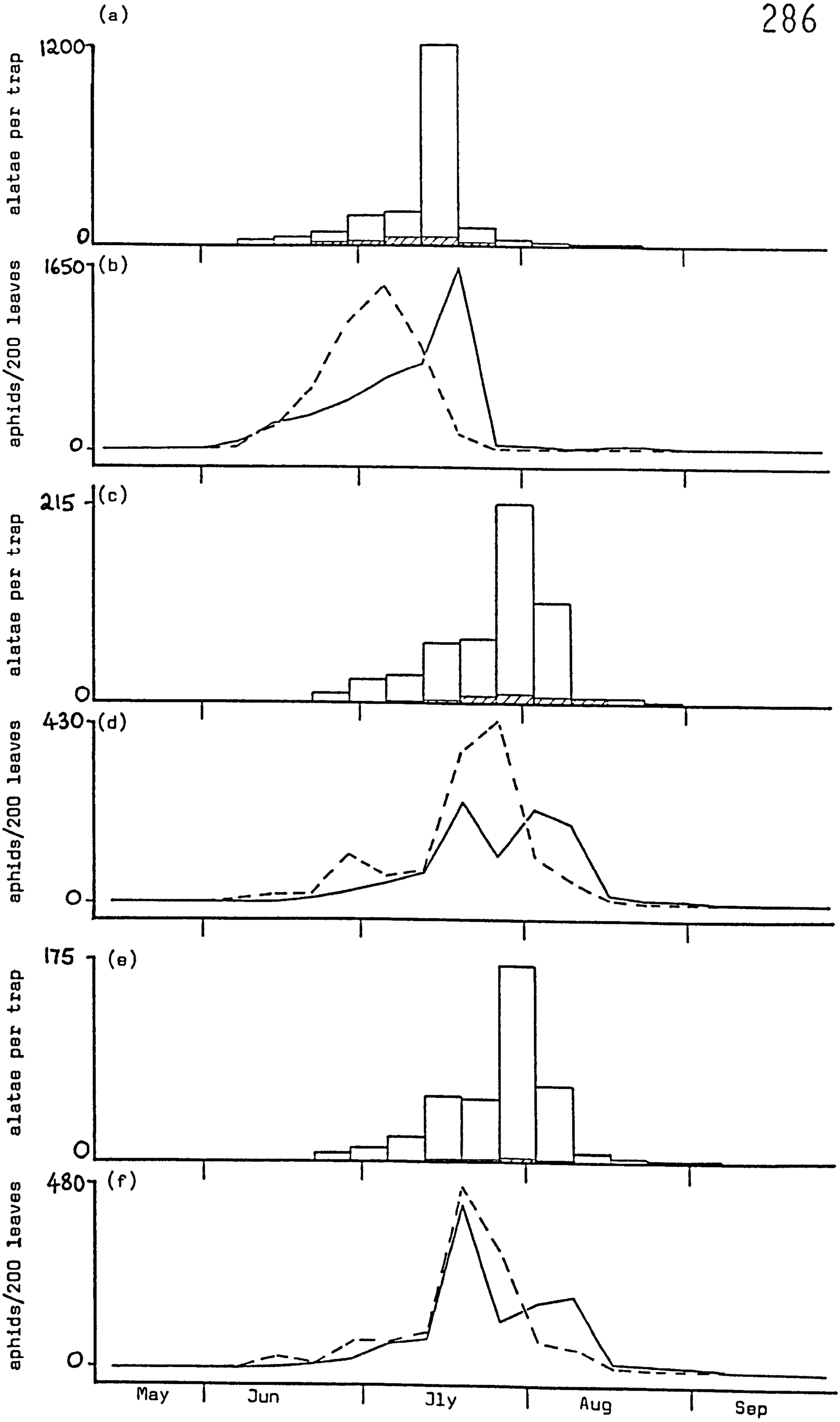

(a)
1200
0
alatae per trap
(b)
1650
0
aphids/200 leaves
(c)
215
0
alatae per trap
(d)
430
0
aphids/200 leaves
(e)
175
0
alatae per trap
(f)
480
0
aphids/200 leaves
May
Jun
Jly
Aug
Sep

Figure 136:

Production and migration of alatae, WM 110 section 1

(a) Alatae per trap, 1982

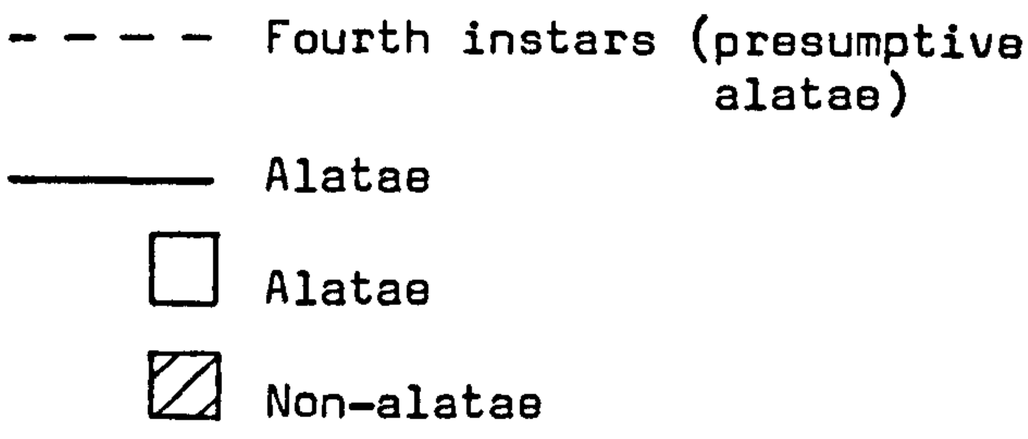
(b) Fourth instars (presumptive alatae) and alatae on windbreak

(c) Alatae per trap, 1983

(d) Fourth instars and alatae on windbreak, 1983

(e) Alatae per trap, 1984

(f) Fourth instars and alatae on windbreak, 1984



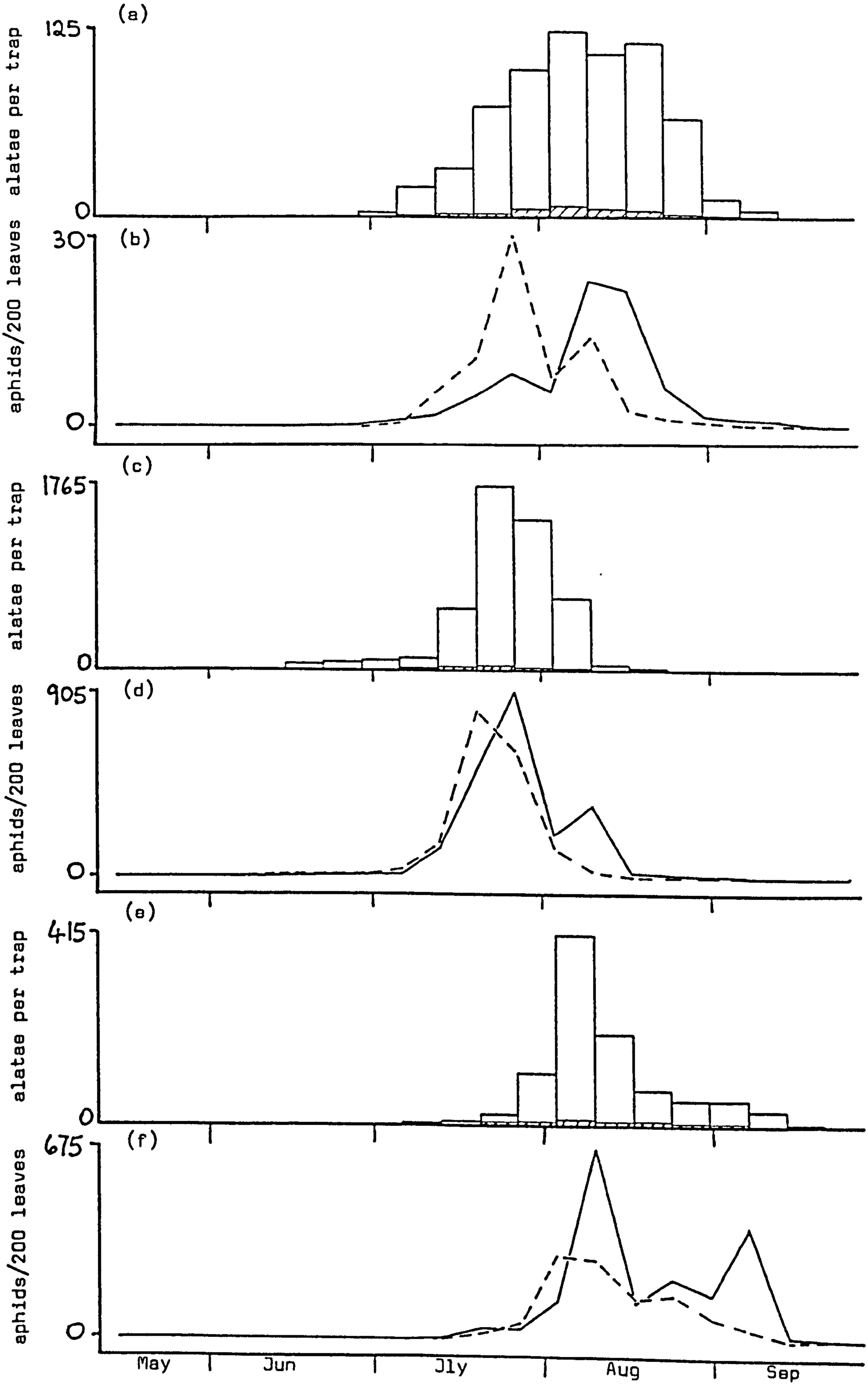

(a)
125
0
(b)
30
0
aphids/200 leaves alatae per trap
(c)
1765
0
(d)
905
0
(e)
415
0
(f)
675
0
May
Jun
Jly
Aug
Sep

Figure 137:

Production and migration of alatae, WM 110,
sections 2 and 3

(a) Alatae per trap, section 2, 1983

(b) Fourths and alatae on windbreak, section 2, 1983

(c) Alatae per trap, section 2, 1984

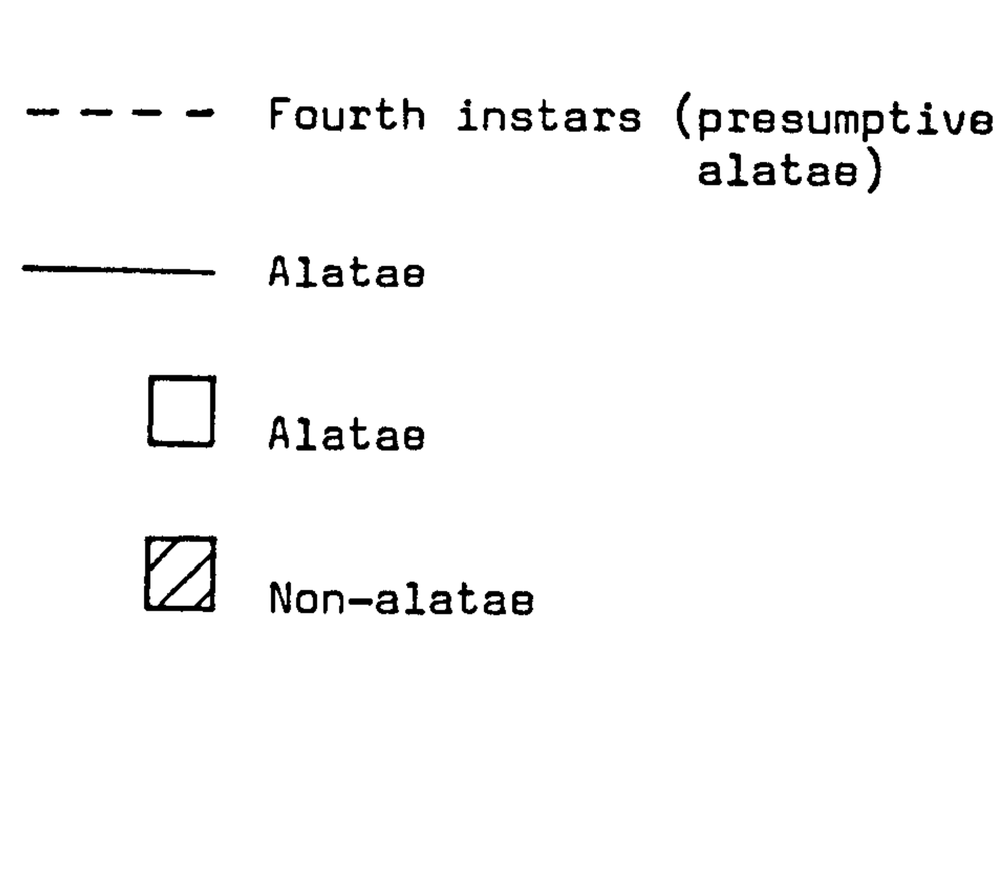
(d) Fourths and alatae on windbreak, section 2, 1984

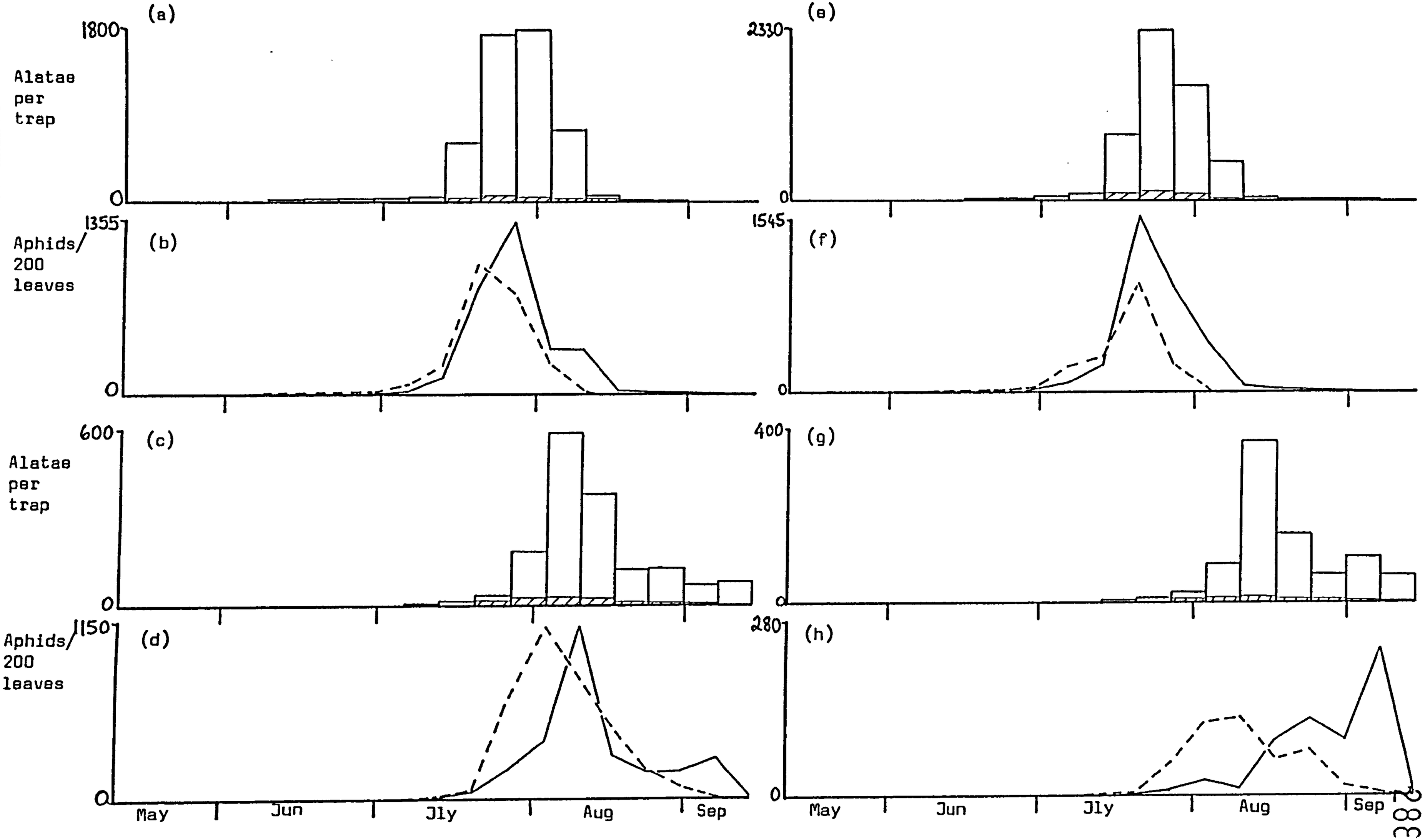
(e) Alatae per trap, section 3, 1983

(f) Fourths and alatae on windbreak, section 3, 1983

(g) Alatae per trap, section 3, 1984

(h) Fourths and alatae on windbreak, section 3, 1984




(a)
1800
Alatae per trap
0
(e)
2330
0
1355
Aphids/ 200 leaves
(b)
0
1545
(f)
0
600
(c)
Alatae per trap
0
400
(g)
0
150
Aphids/ 200 leaves
(d)
0
280
(h)
0
May
Jun
Jly
Aug
Sep
May
Jun
Jly
Aug
Sep

This is shown in fig.136 for WM110 section 1. In 1983 when the initial aphid numbers were higher than in 1982 or 1984, fourth instars (presumptive alatae) appeared earlier and alatae were recorded upon the traps earlier than in either of the other two years. The numbers of fourth instars on the windbreak were greatest in 1983 and the numbers of alatae caught on the traps similarly so. This suggests that when population numbers are high, migratory flight is also greater. In 1983 the peak number of alatae on the traps was 2.2 times that of the fourths on the windbreak. In 1984 when numbers were lower this was only 1.3 times, a highly significant difference ($\chi^2 = 25.82$, $p < 0.001$). These findings support the results of laboratory experiments (table 46) in which flight tendency was greatest in crowded conditions. There was a marked seasonal difference in flight activity between the years. Flight activity in 1983 was earlier than in 1982 or 1984 and this was also shown by sections 2 and 3 (fig.137). When the population density was greater, flight occurred earlier in the season thus resulting in early population peaks, as reported in chapter 2. The distribution of flight from WM110 section 1 in 1984 was very different from that in 1983 (Kolmogorov-Smirnov, Dmax = 0.372, $p < 0.001$) for example.

The sticky traps placed within the tree canopy gave an indication of the trivial flight of P.alni. The results for these traps gave a very similar pattern to those placed to register migratory flight (fig.138). A peak in alata abundance on the traps was preceded by a peak in fourth instar (presumptive alatae) abundance on the windbreak.

At both heights and in both years there was a strong relationship between the number of alatae caught on traps in the canopy and those on traps at the orchard edge (figs.139 and 140). Thus the 'intercanopy' flight was not a variable proportion of the migratory flight. However, the different form of the graphs in fig.139 and 140 does suggest that

Figure 138:

Production and migration of alatae

WM 110 section 2, 1983 and 1984

(a) Alatae per trap, 3.5m, 1983

(b) Fourths and alatae on windbreak, 3.5m, 1983

(c) Alatae per trap, 3.5m, 1984

(d) Fourths and alatae on windbreak, 3.5m, 1984

(e) Alatae per trap, 7.5m, 1983

(f) Fourths and alatae on windbreak, 7.5m, 1983

(g) Alatae per trap, 7.5m, 1984

(h) Fourths and alatae on windbreak, 7.5m, 1984

- - - - Fourth instars (presumptive alatae)

——— Alatae

□ Alatae

▨ Non-alatae

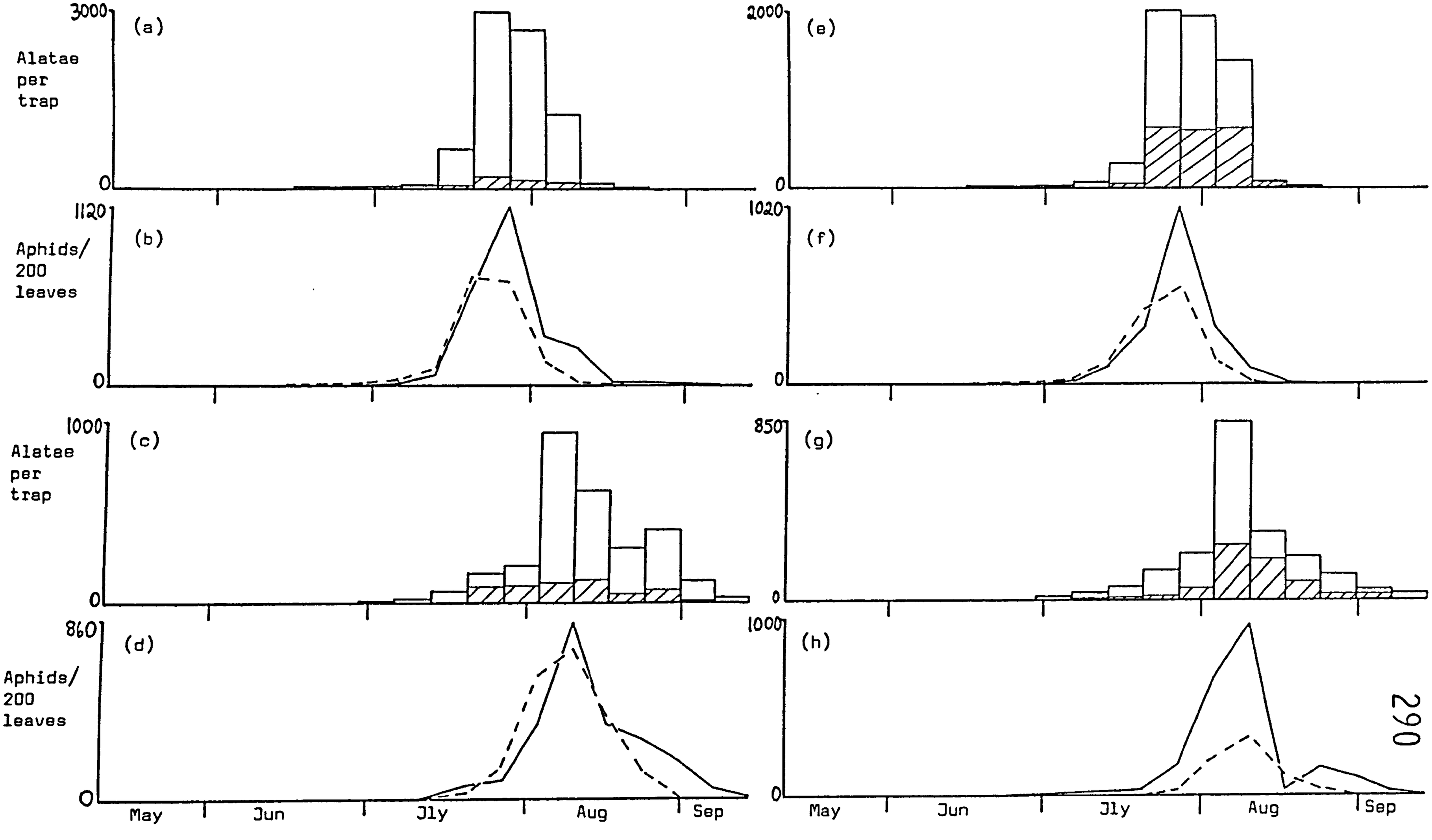

3000
(a)
Alatae per trap
0
1120
(b)
Aphids/ 200 leaves
0
1000
(c)
Alatae per trap
0
860
(d)
Aphids/ 200 leaves
0
May
Jun
Jly
Aug
Sep
2000
(e)
0
1020
(f)
0
850
(g)
0
1000
(h)
0
May
Jun
Jly
Aug
Sep

Figure 139

Relationships between the number of alatae caught on canopy traps and those on orchard edge traps, 1983

(a) 3.5 m

regression line: $\log y = 0.84 \log x + 0.32$

$r = 0.986$, d.f.= 10, $p < 0.001$

(b) 7.5m

regression line: $\log y = 0.88 \log x + 0.26$

$r = 0.987$, d.f.= 10, $p < 0.001$

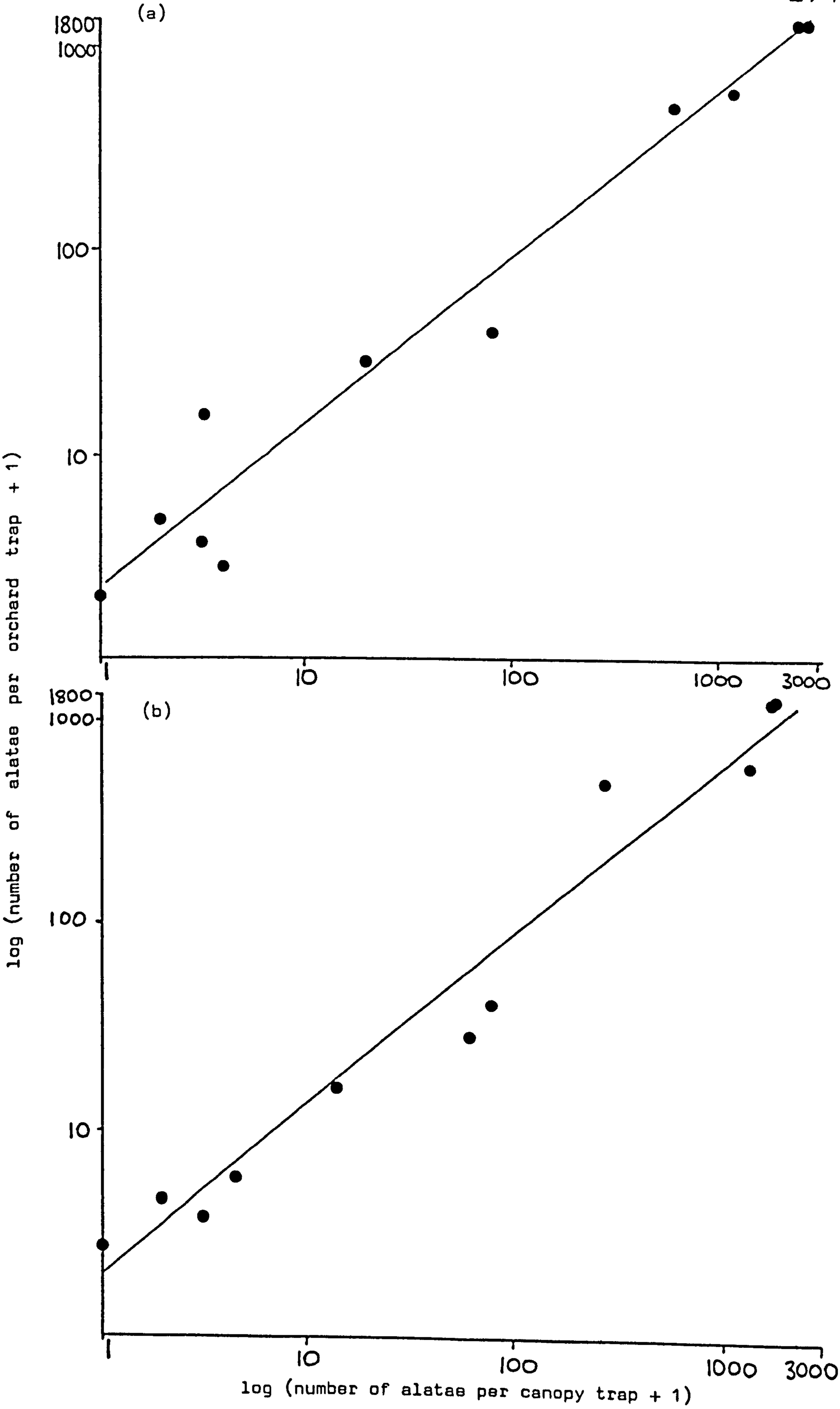

(a)
1800
1000
100
10
1
10
100
1000
3000
(b)
1800
1000
100
10
1
10
100
1000
3000
log (number of alatae per canopy trap + 1)
log (number of alatae per canopy trap + 1)

Figure 140:

Relationships between the number of alatae caught on canopy traps and those on orchard edge traps, 1984.

(a) 3.5m

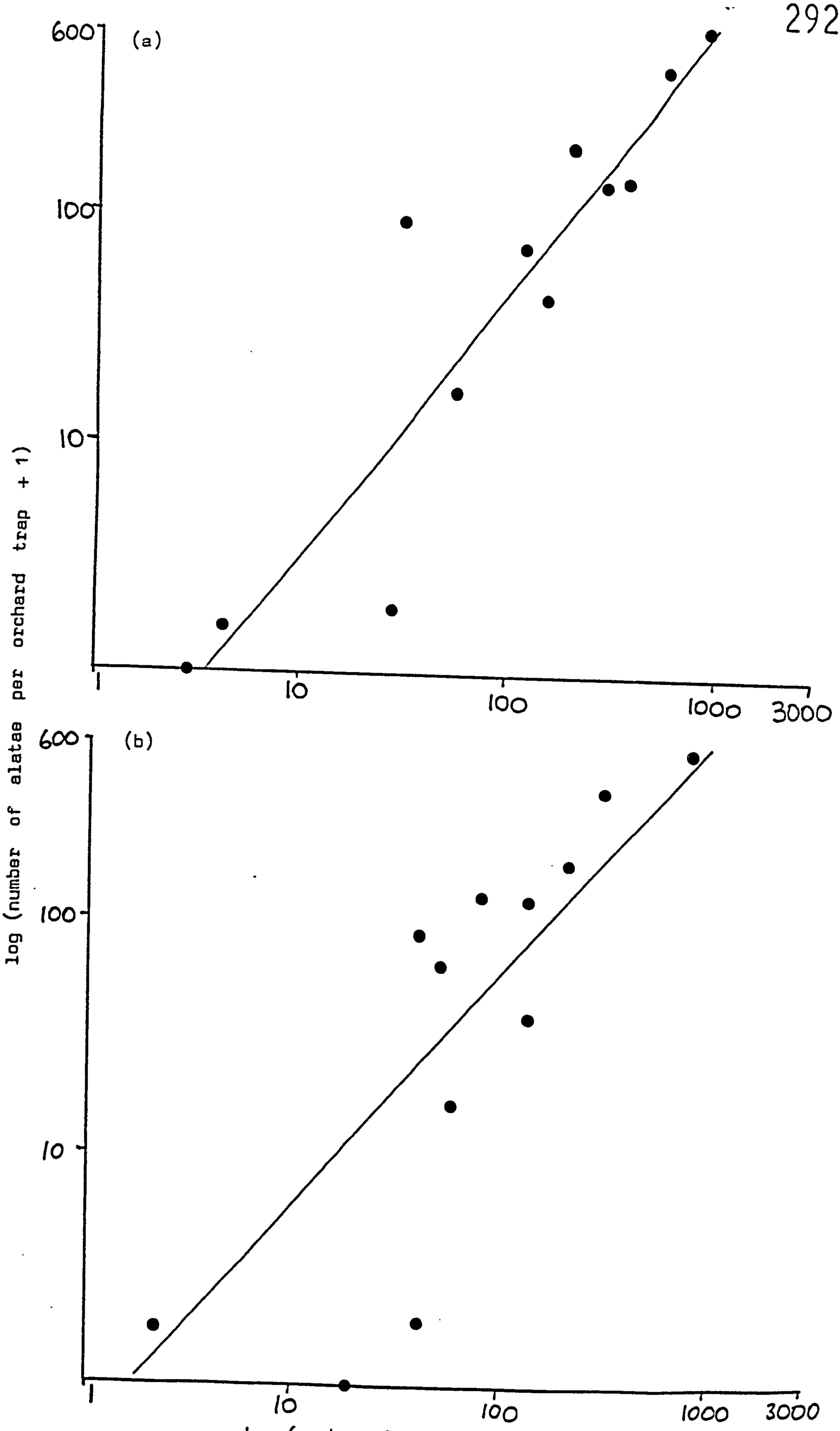
regression line: $\log y = 1.04 \log x - 0.42$

$r = 0.926$, d.f. = 10, $p < 0.001$

(b) 7.5m

regression line: $\log y = 1.13 \log x - 0.54$

$r = 0.839$, d.f. = 10, $p < 0.001$


(a)
600
100
10
1
10
100
1000
3000
log (number of alatae per orchard trap + 1)
(b)
600
100
10
1
10
100
1000
3000
log (number of alatae per canopy trap + 1)

P.alni indulges in trivial flight to a minor extent. In 1983 when numbers were high, the ratio of alatae on the orchard traps to those in the canopy was higher than in 1984, shown by the regression line cutting the y axis at x = 0 (fig.139). In 1984 numbers tended to be greater on the canopy traps, shown by the regression line cutting the x axis at y = 0 (fig.140). This suggests that in 1983 there was a predominance of migratory flight, due to the high population density. In 1984 when the density was lower there tended to be more flight within the canopy than migration away from it. Thus it appears that P.alni indulges in trivial flight, but this is secondary in nature to migratory flight.

Non alate individuals were recorded on all traps but in general, numbers were very low compared with alatae (figs.135-137). The greatest recorded proportion was on WM110 section 3 in 1983, where non-alates reached 6.3% of the alates recorded (fig.137c). On the canopy traps in 1983, non-alates represented 7.0% of the alates at 3.5m; a similar proportion ($d = 1.73$, $p > 0.05$). However, at 7.5m, the proportion was greatly increased to 37.1% ($d = 39.8$, $p < 0.001$). Therefore, there was a greater mortality due to wind at 7.5m, as a result of the height and this was a likely explanation for the failure of populations at 7.5m to reach the levels achieved at 3.5m or 0 - 1.5m (sections 2.5.11 and 2.5.12).

3.3.4. Suction trap records

The total number of aphids caught in suction traps for the Rothamsted Insect Survey for the years 1972-1984 are given in fig.141a, (Wye) and 141c (Silwood Park). It can be seen that the aphid is considerably more abundant in the Wye area compared to Silwood Park. The dates of the peak sample catch are shown in fig.141b (Wye) and 141d (Silwood). Although there appears to be oscillations in abundance from year to year, the peak date of abundance was fairly constant. There was no relationship between

Figure 141:

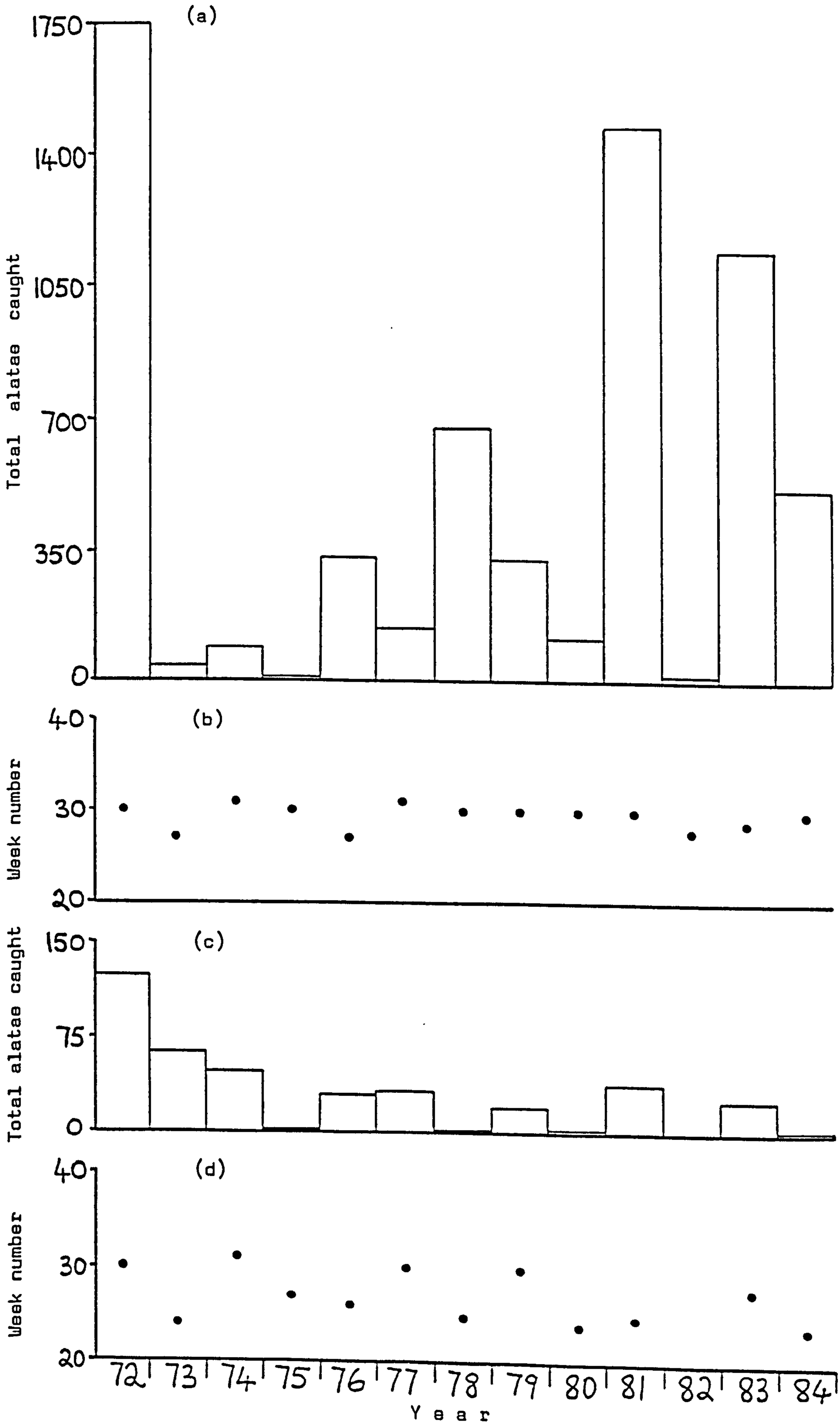
Suction trap records of P.alni 1972-1984

(a) Total numbers of alatae recorded at Wye each year

(b) Date of peak catch, Wye

(c) Total numbers of alatae recorded at Silwood Park each year

(d) Date of peak catch, Silwood


(a)
1750
1400
1050
700
350
0
Total alatae caught
(b)
40
30
20
Week number
(c)
150
75
0
Total alatae caught
(d)
40
30
20
Week number
72
73
74
75
76
77
78
79
80
81
82
83
84
Year

the peak date of abundance and the total aphids trapped in any one year (Wye, r= 0.172,d.f.11, $p > 0.05$; Silwood r = 0.427,d.f.10, $p > 0.05$).

There was a good relationship between the date of first capture and the total number caught at Wye (r = -0.722,d.f.11, $p < 0.01$) indicating that alatae were trapped earlier in years when the aphid was abundant. There was no relationship at Silwood (r= 0.334,d.f.10, $p > 0.05$) but the positive nature of r suggested that in this locality where the aphid is relatively rare alatae were flying later in years when they were most abundant. These results reflect the aphid sampling well; at East Malling where the aphid was abundant (equivalent of Wye) alatae flew earlier when the initial population was high and numbers attained were high. At Lyne where the aphid was rare (equivalent of Silwood) alatae were produced earlier when initial numbers were high, but these numbers were lower than late-peaking populations.

3.4. DISCUSSION

Crowding appears to affect the flight behaviour of P.alni once the aphid has moulted to maturity. Alatae becoming mature in conditions of low population density do not fly as readily as those when the population level is high. Similar reactions have been reported for D.platanoidis (Dixon 1969), M.viciae (Dixon et al, 1968) and E.tiliae (Kidd,1977). This lends support to the hypothesis that migration in aphids is a response to current adversity (Dixon, 1969, 1985a). In field situations, the conditions of over population which cause alata production may no longer prevail when the aphid becomes adult. Thus to stay on the tree would be more advantageous than to fly and possibly fail to find another host plant.

The tendency to fly diminishes with increasing age of the aphid. In D.platanoidis this has been correlated with diminishing fat content (Dixon 1969); the main energy reserve of aphids. It is likely that

a similar loss in fat occurs in P.alni. In this aphid, embryos begin to mature soon after moulting. As the majority of alatae fly in the first day or two of adult life, such maturation would occur soon after flight. Thus upon arrival on a suitable host plant reproduction can begin almost immediately. The weight of an alata increases dramatically after moulting (fig.134) and thus the increase in weight and embryo maturation may lessen the tendency to fly. Alatae retain the ability to fly throughout their lives, similar to D.platanoidis (Dixon,1969) and in contrast to species such as A.fabae amd M.viciae in which wing muscles are autolysed (Dixon,1973). Thus although the ability to fly is not lost it is considerably diminished throughout adult life. A similar situation occurs in D.platanoidis (Dixon, 1974) in which it was shown that large (by weight) aphids fly less readily than small ones.

The maturation of embryos after moulting is a likely explanation for the tendency of aphids not to deposit nymphs before flight. (Table 49). Aphids moult to adulthood without any mature embryos inside. The majority of these fly in the first day of life when crowded. When isolated the tendency to fly is lessened and after maturation, nymphs begin to be produced. The fact that some alata fly after producing nymphs confirms that the ability is not lost. Alatae of other aphids will reproduce before flight. Examples are D.platanoidis (Dixon,1969) and A.fabae (Johnson,1958; Shaw,1970b).

Aphids do not fly to exhaustion before alighting, and take flight again if they settle on a non-host plant (Dixon 1973). There is little evidence to suggest that aphids alight selectively and it is likely that they stay for prolonged periods on suitable plants and depart quickly from others. On landing, aphids invariably probe the leaf surface. This probe determines whether the aphid will leave. Certain arrestants have been identified, such as sparteine for A.spartii on broom (Smith, 1966),

sinigrin for B.brassicae on cabbage (Wensler,1962) and cavarone for Cavariella aegopodi (Scopoli) (Chapman, Bernays and Simpson, 1981). The uneven distribution upon the three alder species in a greenhouse suggests that alatae took off again from A.incana and A.cordata and that the arrestant stimulus of these two species was not as strong as that of A.glutinosa. This may explain the uncommon occurrence of the aphid on these two alders in the field, such as at Lyne and on LF126. Only when these species are in close proximity to A.glutinosa from which very high numbers of alatae are leaving, do they become colonized.

In field situations, migratory flight appears to dominate over trivial flight. Over population leads to migratory activity resulting in dispersal to other less populated trees. When the population density on the windbreak is different between two years, the pattern of flight is different and reflects that of the density. The strong relationship between sticky trap catches in the canopy and those at the orchard edge is in contrast to that observed for D.platanoidis (Dixon, 1969). The sycamore aphid shows marked seasonal changes in its distribution up the tree and trivial flight at various times serves to redistribute the aphid, from top to lower canopy in early summer and from lower to top in autumn. This redistribution causes trivial flight to be a variable proportion of migratory activity. In P.alni trivial flight occurs only to a minor extent and there appears to be little redistribution up the tree. The numbers of aphids in the middle and top canopy are well correlated with those in the lower canopy:

	1983	1984
	r	r
bottom/middle	0.993	0.961
bottom/top	0.970	0.929

(all values of r significant at $p < 0.001$)

There are no differences in intracanopy distribution patterns of P.alni. Similar results for other tree dwelling aphids were reported for

Monellia caryella (Fitch) and Monelliopsis nigropunctata (Granovsky) on pecan (Edelson and Estes, 1983). Thus P.alni shows a contrasting vertical distribution to D.platanoidis and has no need of trivial flight to redristibute itself up or down a tree.

Suction trap data showed similar patterns to that obtained in the orchard. In localities where the aphid is abundant (East Malling and Wye) alatae flew earlier in years when their numbers were greatest, again suggesting that population pressure was causing migration. In localities where the aphid was rare(Lyne and Silwood) the converse was true. This reflected the population dynamics of P.alni well in these two localities (chapter 2).

The aphid was considerably more abundant at Wye than at Silwood in every year. It is likely that this is a result of the amount of alder planted in Kent to act as windbreaks in the many orchards. It is possible if a number of traps were used that the sources of P.alni migrations in Kent could be established. This may produce a pattern of population patches (i.e.orchards) similar to that observed for Phorodon humuli (Schrank) emerging from hop gardens (Taylor, Woiwood and Taylor, 1979). Suction trap results for 1966-1983 were examined for Long Ashton (Bristol), Hereford, Shardlow (Derbyshire) and Rothamsted (Hertfordshire). It was noticeable that the only locality in which the aphid was at all numerous was Hereford - the other major orchard area in Britain.

Chapter 4 SEXUAL MORPH PRODUCTION AND OVERWINTERING IN *P.alni*

4.1. SEXUAL MORPH DETERMINATION

4.1.1. Introduction

The ability to form sexual females (oviparae) and males is widespread in aphids from temperate climates. A number of factors influence this ability. Environmental photoperiod and temperature are important but innate factors such as parental type and time-dependent inhibitors also may play a part. It has long been known that the appearance of sexual morphs in autumn is in response to short day-lengths and low temperatures. This was first discovered by Marcovitch (1924) working with Aphis forbesi Weed. Oviparae were produced prematurely in summer by restricting normal daylight and their appearance later in the season postponed by extending the daylight. Many other aphids have been shown to have similar photoperiodic responses. Although associated with short days, the process of sexual production is actually triggered by long nights (Lees,1973). Aphids which have been shown to respond in this way include Aphis chloris Koch (Wilson, 1938), B.brassicae (Bonnemaison, 1951), A.pisum (Kenten, 1955; Lamb and Pointing, 1972) and M.viciae (Lees, 1959). These aphids are all monoecious (non-host alternating). Heteroecious aphids are also responsive to photoperiod. Examples are A.fabae (de Fluiter, 1950), M.persicae (Bonnemaison,1951; Blackman, 1975) and R.padi (Dixon and Glen, 1971). In these host-alternating aphids winged males and gynoparae are produced. These fly to the primary host, where the gynopara produces only oviparae (Hille Ris Lambers, 1966). A few species of aphid respond to changes in their food supply which also signal the onset of adverse conditions. Such an aphid is Dysaphis devecta (Walker) on apple (Forrest, 1970).

In many aphids, fundatrices which hatch from overwintering eggs cannot be readily induced to give rise to sexual morphs whereas later generations more easily do so. This phenomenon was termed 'facteur fondatrice' by Bonnemaison (1951) and 'interval timer' by Lees (1960). Interval timers

affecting sexual morph production have been shown to exist in many species of aphid, such as M.viciae (Lees,1960) and A.pisum (Lamb and Pointing,1972). In these the interval timers operate independently of daylength. However, in D.platanoidis (Dixon 1971e) there are two interval timers; one sensitive to daylength controlling ovipara production and one insensitive controlling the production of males. In E.tiliae (Dixon,1972a) there are also two interval timers, but both are sensitive to day length, although responding in different ways.

M.euphorbiae is an interesting aphid as it appears to possess features common to monoecious and heteroecious species. In a study of this aphid (MacGillivray and Anderson, 1964) it was found that under short day conditions apterous adults produced apterae, alatae, males and oviparae. These alate viviparae, produced from uncrowded parents produced in turn only oviparae. Thus they were analogous to the gynoparae of a heteroecious aphid. At the same time, the ability of these same parents to produce oviparae is a characteristic of monoecious species.

Some aphids do not produce sexuales but survive the winter as parthenogenetic virginoparae in sheltered situations. An example is Myzus ascalonicus Doncaster (Hille Ris Lambers, 1966). In other species anholocyclic (no sexual reproduction) and holocyclic (life cycle involving sexual reproduction) strains are found, even together in the same locality (Lees, 1966).

The term 'reproductive sequence' is used to refer to the pattern of appearance of morphs throughout the reproductive period of a virginoparous aphid (Lamb and Pointing, 1975). As the embryos in different ovarioles appear to keep in step during development, the time of parturition probably reflects the sequence in which the eggs were ovulated (Lees, 1966). In M.viciae, males are born in the middle of the reproductive life of the parent virginopara (Lees, 1959). In A.pisum, males tend to be born last (Kenten,

1955; Lamb and Pointing, 1975). In R.padi (Dixon and Glen, 1971) males are produced after gynoparae, after a certain number of days have elapsed.

In this section the production of sexual morphs in P.alni is examined. Field observations and studies are reported, together with experiments at controlled temperatures in a growth room.

4.1.2. Materials and methods

Field populations have been studied and the appearance of sexual morphs recorded. Data from Lyne and East Malling was extremely similar for all windbreaks and trees sampled within and between years. The results for each sampling date were thus averaged.

Aphids were confined upon leaves on the windbreaks in cages similar to that described by Noble (1958). Aphids used were those produced from the experiments reported previously for alate production in P.alni. The lineage used was cr/i/i/i with the second generation alate and the third and fourth apterous. It was felt that this was a fair reflection of a typical field situation of a high initial population followed by low numbers after a decline. The fourth generation adults so produced were reared on the windbreak and their offspring reared in weekly batches. The first offspring from these adults were reared in the same way so that the production of these when adult was synchronous with that of their parents. Similarly the first offspring of these began producing whilst their mothers were still doing so. The experimental design on two windbreaks was thus:

Dates	WM 110	LF 125
17/8 – 18/10	A: Reproduction of 4th gen. i.e.rearing of 5th gen.	B: Reproduction of 5th gen. i.e.rearing of 6th gen.
10/9 – 25/10	C: Reproduction of 5th gen. i.e.rearing of 6th gen.	D: Reproduction of 6th gen. i.e.rearing of 7th gen.

A feature of this experiment was the longevity of the fourth generation, enabling three generations to be studied simultaneously. Batches of offspring were obtained by leaving an aphid to reproduce on a leaf and then subsequently removing it to another leaf leaving the offspring produced behind. The morphs of all the offspring produced were determined at adulthood. Individual progeny sequences were followed so that the proportions of aphids producing 'families' containing (a) virginoparae only; (b) virginoparae and males; (c) virginoparae and oviparae; (d) virginoparae, oviparae and males and (e) oviparae and males, could be obtained. This method of result recording is preferable to that of pooling the results from many parents (Lees,1959) as it measures accurately the response of the parents. In this study both methods were used to describe the morphs produced, similar to Lamb and Pointing (1972).

Aphids were caged upon alder saplings at constant temperatures of $10^{o}C$, $15^{o}C$ and $20^{o}C$. Successive generations were reared at each temperature in a photoperiod of 16h light/8h dark ('long day'). At $15^{o}C$ the fourth, fifth and sixth generations were reared in short conditions of 12h light/12h dark. The timing of the maternal response to photoperiod was examined by switching one batch of adult aphids from short day conditions to long day and then back to short days.

4.1.3 Results

In the field, the first males and oviparae appeared in late September and early October respectively (fig.142). Males generally preceded the appearance of oviparae and were not found after late October. At this time of the year it takes 17-22 days for P.alni to reach maturity (chapter 5) and so these were born at the end of August when day length is about $13\frac{3}{4}$ hours. Although P.alni hatches from the egg in late April, it is not present in the field early in the year at a comparable day length. The day length at egg

Figure 142:

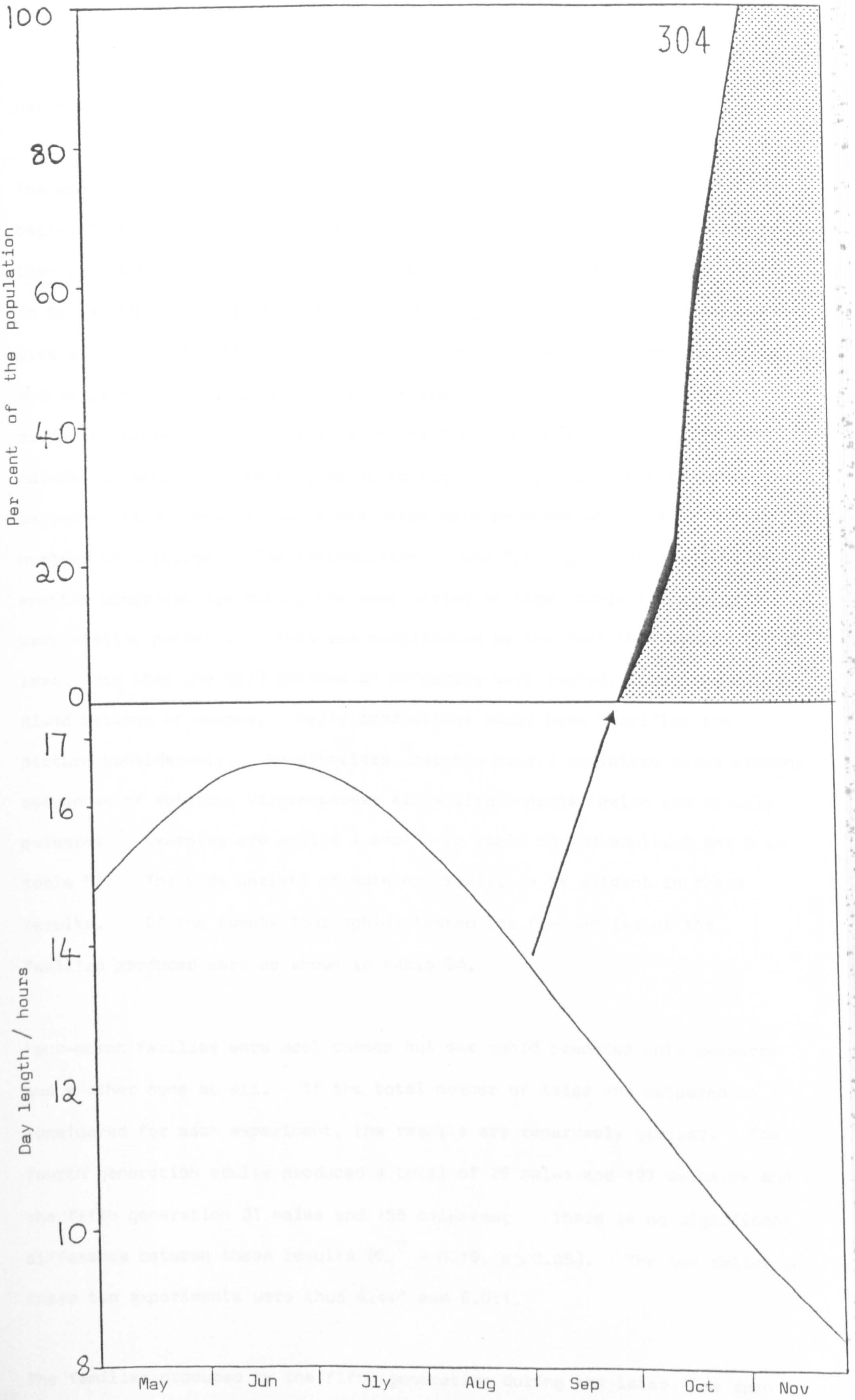
The relationship between the appearance in the field of sexual morphs of P.alni and daylength

virginoparae

males

oviparae

Arrow represents birth of first sexuales.


100
80
60
40
20
0
Per cent of the population
304
17
16
14
12
10
8
Day length / hours
May
Jun
Jly
Aug
Sep
Oct
Nov

hatch time is about 14½ hours.

The appearance of sexual morphs was followed closely in the field by caging 12 aphids of three generations and recording the forms of the progeny they produced. The results of the individual progeny sequences are given in tables 50 - 53. It can be seen that P.alni apterous virginoparae may give birth to a 'family' containing apterous and alate virginoparae, males and oviparae. This appears to be the order in which the morphs are produced (table 50). The adults of the fourth generation all produced batches of apterous offspring prior to August 28th. In the subsequent period small numbers of alatae and males were produced and finally larger numbers of oviparae. The reproduction of the fifth generation adults on another windbreak but during the same period of time (table 51) showed a very similar pattern. This was complicated by the fact that weekly (or at least more than one day) batches of offspring were reared, thus producing mixed batches of morphs. Daily productions would have clarified the picture considerably. Nevertheless, certain adults exhibited clear progeny sequences of apterous virginoparae; alate virginoparae; males and finally oviparae. Examples are adults 1 and 10 in table 50 and adults 2 and 3 in table 51. The wide variety of maternal reactions is evident in these results. Of the twenty four aphids tested the frequencies of the families produced were as shown in table 54.

Four-morph families were most common but one aphid produced only oviparae and another none at all. If the total number of males and oviparae is considered for each experiment, the results are remarkably similar. The fourth generation adults produced a total of 29 males and 127 oviparae and the fifth generation 31 males and 156 oviparae; there is no significant difference between these results ($\chi_1^2 = 0.19$, $p > 0.05$). The sex ratios in these two experiments were thus 4.4:1 and 5.0:1.

The families produced by the fifth generation during the later time span

Table 50 PROGENY RECORDS OF INDIVIDUAL APTEROUS VIRGINOPARAE OF THE FOURTH GENERATION CAGED ON WM 110

Number in brackets after parent number is number of apterous offspring produced up until 22/8

Number of parent:	1 (12)				2 (15)				3 (24)				4 (17)				5 (4)				6 (28)			
Nymphs born between:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
22/8 - 28/8	6				4				2				4				4				2			
28/8 - 30/8	6				4				2		1					1	3				2			
30/8 - 2/9	1	1	1		1		1	2			1					2			2		1			
2/9 - 12/9			1	2			1	3				2				4			2				1	1
12/9 - 29/9				3				2				1				3			2	1			2	1
29/9 - 12/10				1				2				1				3			1					3
12/10- 18/10				1				2				4				2			1					6
Totals	13	1	2	7	9	0	2	11	4	0	2	8	4	0	0	15	7	0	6	1	5	0	3	11

Number of parent:	7 (10)				8 (17)				9 (26)				10 (31)				11 (13)				12 (14)			
Nymphs born between:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
22/8 - 28/8	4	2			4				4				5				4	1			4			
28/8 - 30/8			1			1			5				5	1			4			1	2			
30/8 - 2/9			3				1					2			2					1				1
2/9 - 12/9				2			1	2				3				2			4					3
12/9 - 29/9				4			1	1				5				4			1	2				4
29/9 - 12/10				13				1				16				3				2				10
12/10- 18/10				2				2				1				2				2				3
Totals	4	2	4	21	4	1	3	6	9	0	0	27	10	1	2	11	8	1	5	8	6	0	0	21

Table 51 PROGENY RECORDS OF INDIVIDUAL APTEROUS AND ALATE VIRGINOPARAE OF THE FIFTH GENERATION CAGED ON LF 125

Number of parent:	1				2				3				4				5 (Al)				6			
Nymphs born between:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
22/8 – 27/8	4				10	3			11	3			6	1					1		9	2		
27/8 – 31/8	7				4				1		5	3	1	1					5		3			
31/8 – 3/9	6		1			2	2				2		1	2					6		3			1
3/9 – 7/9			2					5				2				2								3
7/9 – 14/9				3				3			1	1				3								2
14/9 – 24/9				4				5				2				4								3
24/9 – 1/1)				3				3				6				5								4
Totals	17		3	10	14	5	2	16	2	3	8	14	7	4		14			12		15	2		13

Number of parent:	7				8				9				10				11				12			
Nymphs born between:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
22/8 – 27/8	1				1	2			3	2							1	1			6	2		
27/8 – 31/8	3	2			2	7			3							1	4				1			
31/8 – 3/9	4				4						2					3	5	1					2	
3/9 – 7/9				1				2			1					2				2			1	4
7/9 – 14/9				1				2				6				3				4				1
14/9 – 24/9				1				3				4				5				3				2
24/9 – 1/10				2				3				8				6				13				7
Totals	8	2		5	7	9		10	6	2	3	18				20	10	2		22	7	2	3	14

Table 52 PROGENY RECORDS OF INDIVIDUAL APTEROUS AND ALATE VIRGINOPARAE OF THE FIFTH GENERATION CAGED ON WM 110

Number of parent:	1				2				3 (Al)				4				5				6 (Al)			
Nymphs born between:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
10/9 – 17/9	1						2				1				1				1				2	
17/9 – 20/9							3				1					1			1	2			4	
20/9 – 24/9			9				2				2				5	3			3	1			2	1
24/9 – 28/9			4	3			1	1			1				3	2			4	2			3	3
28/9 – 12/10			7	2				2				3			5	1				12			1	2
12/10– 18/10				4				3				4			3	2				6				4
18/10– 25/10				3				3				2				3				7				3
Totals	1		20	12			8	9			5	9			17	12			9	30			12	13

Number of parent:	7				8				9				10				11				12			
Nymphs born between:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
10/9 – 17/9			1				1				2				1				1				1	
17/9 – 20/9			1				1				3				1	1			1				1	
20/9 – 24/9				4			1				1	1				2				1			1	2
24/9 – 28/9				1			2				2	2			2	2				3			4	1
28/9 – 12/10				11			3				2	4			2	5				5				4
12/10– 18/10				5				4				8			2	4				6				3
18/10– 25/10				4				5				4				5				4				3
Totals			2	25			8	9			10	19			8	19			2	19			7	13

Table 53 PROGENY RECORDS OF INDIVIDUAL APTEROUS VIRGINOPARAE OF THE SIXTH GENERATION CAGED ON LF 125

Number of parent:	1				2				3				4				5				6			
Nymphs born between:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
10/9 - 14/9			2		1		1				3				3		1	1	2				2	
14/9 - 17/9			4				1				1				2				2				1	
17/9 - 20/9			4				2	4			1				1				6	1			2	
20/9 - 24/9			1	2				5			1								3	3			1	
24/9 - 1/10			1	7			2	14			2								12	13			4	2
1/10- 12/10				10			3	10			4									8			1	2
12/10- 25/10				4				5			1									4				1
Totals			12	23	1		9	38			13		6				1	1	25	29			11	5

Number of parent:	7				8				9				10				11				12			
Nymphs born between:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
10/9 - 14/9	1		1				2				6				3				1				3	
14/9 - 17/9			1					9			5				2					7			1	
17/9 - 20/9			4					7			4				1				1	1			1	3
20/9 - 24/9			1	2				4			5				3					6				2
24/9 - 1/10			1	2				12			6	8			5					14				4
1/10- 12/10			1	2				12				11			1					3				5
12/10- 25/10				2				4				3			4					2				2
Totals	1		9	8			2	48			26	22			19				2	33			5	16

Table 54 THE FREQUENCY OF DIFFERENT FAMILIES PRODUCED BETWEEN AUGUST 27TH AND OCTOBER 1ST

Family	Number	%
Ap,Al,M,Ov	9	37.5
Ap,Al,Ov	5	20.8
Ap,M,Ov	4	16.6
Ap,Ov	3	12.5
Ap,Al,M	1	4.2
Ap,M,Ov	1	4.2
Ov	1	4.2

Table 55 THE FREQUENCY OF DIFFERENT FAMILIES PRODUCED BETWEEN SEPTEMBER 10TH AND OCTOBER 25TH

Family	Number	%
Ap,Al,M,Ov	1	4.2
Ap,M,Ov	3	12.5
M,Ov	17	70.8
M	1	4.2
Ov	2	8.3

were different to those of the earlier period (table 52). Here males were the first morphs to be produced and sequences of these were followed by oviparae. The reproduction of the sixth generation on another windbreak but at the same time showed a very similar pattern (table 53) with small numbers of apterae and alatae produced at the start. A smaller range of families were produced in these experiments (table 55).

On this occasion families consisting of the two sexual morphs were most common and the four-morph family was this time produced only once. The total number of sexuals produced in these two experiments was again similar. The fifth generation adults produced 108 males and 189 oviparae, and the sixth, 107 males and 254 oviparae. These numbers were not different ($\chi_1^2 = 3.34$, $p > 0.05$). In this case the sex ratios were 1.8:1 and 2.4:1, the difference between these and the previous experiment being accounted for by the numbers of males produced. Although the families produced by different generations at the same time were similar, those produced by the same generation at different times were not. The fifth generation during the early time span yielded 31 males and 156 oviparae whereas during the later period it gave 108 males and 189 oviparae. The increased number of males caused these proportions to be very different ($\chi_1^2 = 21.94, p < 0.001$). Thus sexual morph production appeared to depend upon the time of year, not the generation.

As the sexual morphs were produced at similar times regardless of generation number it seems likely that the aphid responds to environmental stimuli. These are likely to be photoperiod and temperature. It is noteworthy that larger numbers of oviparae and males were produced in the course of the later experiment. The early experimental aphids produced virginoparae before the sexual morphs and only oviparae at the end of their lives. As both sets of aphids appeared to produce a sequence of males and then change to ovipara production, it is interesting to compare the total numbers of

males produced in each experiment. Male production was significantly less in the early experiment ($\chi_1^2 = 87.4$, $p < 0.001$). The 'early' adults which produced males in late August, in the fifth and sixth generations may have been responding to environmental cues from mid August onwards. However, those adults of the fifth and sixth generations which produced males in early September were born in mid August at a similar time as the males. The first born of these adults thus became males in response to environmental conditions perceived by the mother in late August. Males in each generation may thus have been produced in response to environmental stimuli at a certain time. It remains to reconcile the differences in the numbers of males produced. A possible factor is food quality which is improving all the time from early August until October. The fourth generation adults were smaller than the fifth having been born in mid July rather than mid August. Smaller aphids are less fecund than larger ones (Dixon and Wratten,1971) thus the smaller number of males produced earlier may be due to the fact that their parents were smaller and less fecund. Another possibility is temperature. High temperature may affect male production. However, the males in each generation were determined at a similar time and so it is unlikely that temperature could have had any effect. Thus the lack of males may be due to the poorer food quality available to the adults in the early experiment.

For each batch of offspring produced in each experiment the average photoperiod during the time the batch was produced was evaluated. Although not entirely accurate, this method gives an indication of the photoperiod at which males and oviparae are produced. The pooled results are presented in table 56. The results of the early experiments are perhaps most meaningful as they indicate when, after virginoparae production, sexual production occurs. It appears that males began to be produced from about $13\frac{3}{4}$ - 14 hours light and oviparae from $13\frac{3}{4}$ hours onwards. Male production reached a peak at about $13\frac{1}{2}$ hours after which it subsided and morphs tended to be all oviparae. No

Table 56 PHOTOPERIOD AND THE PRODUCTION OF MALES AND OVIPARAE OF P.ALNI

Experiment A
Progeny of 4th generation
on WM110

Date	Average Photoperiod	% Males	% Oviparae
22/8–28/8	14.05	0	0
28/8–30/8	13.80	5.1	2.6
30/8–2/9	13.60	45.5	27.3
2/9–12/9	13.20	28.1	71.9
12/9–29/9	12.30	11.1	88.9
29/9–12/10	11.40	0	100.0
12/10–18/10	10.75	0	100.0

Experiment B
Progeny of 5th generation
on LF125

Date	Average Photoperiod	% Males	% Oviparae
22/8–27/8	14.07	1.3	0
27/8–31/8	13.79	18.9	5.7
31/8–3/9	13.58	31.9	8.5
3/9–7/9	13.36	14.8	85.2
7/9–14/9	13.00	3.3	96.7
14/9–24/9	12.44	0	100.0
24/9–1/10	11.89	0	100.0

Experiment C
Progeny of 5th generation
on WM110

Date	Average Photoperiod	% Males	% Oviparae
10/9–17/9	12.81	93.3	0
17/9–20/9	12.48	80.9	19.1
20/9–24/9	12.25	63.4	36.6
24/9–28/9	11.98	60.0	40.0
28/9 12/10	11.40	28.2	71.8
12/10–18/10	10.75	8.6	91.4
18/10–25/10	10.34	0	100.0

Experiment D
Progeny of 6th generation
on LF125

Date	Average Photoperiod	% Males	% Oviparae
10/9–14/9	12.90	69.7	18.2
14/9–17/9	12.68	47.2	52.8
17/9–20/9	12.48	58.1	41.9
20/9–24/9	12.25	28.2	71.8
24/9–1/10	11.89	21.8	78.2
1/10–12/10	11.31	7.8	92.2
12/10–25/10	10.54	0	100.0

males were produced when daylength fell below 13 hours. The fact that in the later experiment males were still produced when the daylength was 12 hours may be due to the fact that the sex of these aphids was determined when their mothers were still nymphs, in late August. Thus these embryos were irreversibly determined as males and were produced before oviparae.

It is interesting that males were not continually produced throughout either experiment. It is unlikely therefore that male production was stimulated by a drop in temperature as production would have continued as the days got colder. Males therefore only appear to be produced when the daylength is between 13 and 14 hours.

In some aphids the males are produced after a certain number of previous offspring or a certain number of days. The number of days from adulthood to the production of the first male and ovipara are listed in table 57. The number of offspring produced before the first male and the number of males before the first ovipara are also given. In the early experiments, a variable number of days elapsed before males were produced and the number of virginoparous offspring also varied(table 57 a and b). The adults became mature on different days, but as the production of males was synchronous (tables 50 and 51), this caused the days elapsed and offspring produced to vary. The number of males produced before an ovipara also varied, from 0 to 6. Thus it appears that neither males or oviparae are produced after a certain time span or amount of offspring. The results for the later experiments (table 57 c,d) confirm this. Even when adults matured on the same day, they did not produce ovipara after a constant number of days (range 2 - 27) or males (range 0-26).

Generations of P.alni were reared continuously throughout the year at $10^{o}C$, $15^{o}C$ and $20^{o}C$ to measure the growth and reproduction of each generation (chapter 5). The light regime used in all these experiments was 16h light/ 8h dark. Under these conditions no sexual forms were ever produced. At

Table 57 THE NUMBER OF DAYS BEFORE AND THE NUMBER OF OFFSPRING PRODUCED BY APTEROUS VIRGINOPARAE BEFORE SEXUAL PRODUCTION

(a)
WM 110

Date became adult on	Number of offspring produced before a male	Number of males produced before an ovipara	Number of days before a male	Number of days before an ovipara
4/8	33	1	29	29
5/8	26	2	25	28
5/8	28	2	23	28
8/8	24	1	22	22
8/8	21			20
8/8	35			23
8/8	32	2	22	20
8/8	20			28
14/8	22	0	19	16
14/8	22	1	16	19
14/8	16	4	14	19
14/8	11	6	16	29

(b)
LF 125

7/8	39	5	20	20
7/8	33			26
7/8	23	3	24	31
7/8	21	3	24	27
8/8	31			26
8/8	36			25
8/8	38	2	23	26
8/8	31	3	23	30
10/8	16	no oviparae	12	
10/8	24			21
10/8	20			23
10/8	26			17

Table 57 (cont.) THE NUMBER OF DAYS BEFORE AND THE NUMBER OF OFFSPRING PRODUCED BY APTEROUS VIRGINOPARAE BEFORE SEXUAL PRODUCTION

(c)
WM 110

Date became adult on	Number of offspring produced before a male	Number of males produced before an ovipara	Number of days before a male	Number of days before an ovipara
8/9	1	13	12	16
8/9	0	8	2	16
8/9	0	5	2	20
8/9	0	1	2	9
8/9	0	8	2	9
15/9	0	2	2	5
15/9	0	8	2	5
15/9	0	6	2	27
15/9	0	2	2	15
15/9	0	2	2	2
15/9	0	1		5
15/9	0	3	2	5

(d)
LF 125

7/9		11		3
7/9				3
8/9	0	11	2	13
8/9	1	4	2	10
8/9	0	no oviparae	2	
8/9	2	10	2	10
8/9	0	10	2	17
8/9	1	7	2	13
8/9	0	2	2	7
8/9	0	26	2	17
8/9	0	1	2	7
8/9	0	5	2	10

20°C a culture was maintained for 18 months and only apterous and alate virginoparae were produced. At 15°C a culture containing apterous virginoparae of the 3rd generation was used to examine the changing response of the mother evident in table 50. Twelve adults were confined upon leaves of A.glutinosa saplings. After a week each adult was removed to another leaf and the offspring produced left. After two weeks the procedure was repeated but at this point the light regime was changed from 16h light/8h dark to 12h light/12h dark. Adults were recaged on different leaves after 7, 14, 21 and 28 days and the batches of offspring produced each week reared to maturity and their morph determined. The experiment was repeated using 4th and 5th generation adults and the pooled results are given in table 58.

The response to the change in photoperiod was the same in each generation; sexual morphs appearing within a week. Few males were produced in the experiment and many aphids appeared to switch from virginopara to ovipara production.

The response to photoperiod is clearly maternal. The first nymphs to be born were irreversibly determined as virginoparae in the previous long day conditions. The progeny sequences would have been considerably clearer had the production of offspring been followed daily. Nevertheless it appears that a few males were produced before the switch to oviparae which occurred within a week. A week is a long time in the life of an aphid and in late summer when daylength is rapidly decreasing the change in light during a week may be quite substantial. In late August when sexual production first occurred, the change in daylength in a week was about 25 minutes.

To examine the flexibility of this switching mechanism, apterous virginoparae were taken from the field on October 1st and placed in constant temperature rooms at 10°C and 15°C at 16h light/8h dark. Their progeny over the next

Table 58

THE PRODUCTION OF SEXUAL FORMS IN THE FOURTH,FIFTH AND SIXTH GENERATIONS IN RESPONSE TO PHOTOPERIOD AT 15°C

Days after short day length (12/12)	Reproduction of: 3rd generation % Virg. (apterous)	% M	% Ov	4th generation % Virg. (apterous)	% M	% Ov	5th generation % Virg. (apterous)	% M	% Ov
-14 - -7	100	0	0	100	0	0	100	0	0
-6 - 0	100	0	0	100	0	0	100	0	0
1 - 7	69.2	7.7	23.1	63.8	5.9	30.3	58.4	6.8	34.8
8 - 14	21.0	2.3	76.7	19.1	1.4	79.5	8.3	0	91.7
15 - 21	0	0	100	0	0	100	0	0	100
22 - 28	0	0	100	0	0	100	0	0	100

45 days was recorded in four batches and the results of individual sequences are given in table 59 a and b.

The aphid has the ability to start producing virginoparae again and this switching process again occurred in the first week. The progeny sequence appeared to be oviparae, apterae, males, alatae and apterae. Apart from the apterae produced after oviparae this is a mirror image of the sequence obtained when the parent switches to sexual production (table 50). A noteable feature of the results at 15°C was the absence of males. It may be that the temperature-inhibiting effect of male production is again apparent, although males were produced in small numbers at 15°C before (table 58).

To examine the flexibility still further, four of the aphids used in the previous experiment were, after 45 days transferred back to the short day conditions of 12h light/12 h dark at 15°C. Their progeny sequences are shown in table 60.

The aphid has the ability to switch again and this switch occurred after about 10 days. The progeny sequence was apterae, alatae, males and oviparae; the same as that observed in the field (table 50). Only one male was produced; a possible result of the relatively high temperature.

4.1.4. Discussion

The sexual morphs consisting of apterous oviparae and winged males of P.alni first appeared in field populations in late September. They were born in late August when the day length was about 13¾ hours. P.alni hatches from the egg in late April at a time when the daylength is about 14½ hours. Although it is not known when in the development of a parent the determination of her embryos occurs, it is obvious that fundatrices do not produce oviparae

Table 59a INDIVIDUAL PROGENY SEQUENCES OF VIRGINOPARAE TAKEN FROM SHORT DAY CONDITIONS AND PLACED IN LONG DAY CONDITIONS, AT 10°C

Number of parent:	1 (A)				2 (A)				3 (A)				4 (A)				5 (Al)				6 (A)			
Nymphs born between day:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
0 - 7	1			2				3				3				3				3				2
8 - 18	1		2		3				4				3				4			2	5	2		
19 - 31	1		4			5	1			3	1			4				2	4			4		
32 - 45	2				1	1			1				1				1					2		
Totals	5		6	2	4	6	1	3	5	3	1	3	4	4		3	5	2	4	5	5	8		2

Number of parent:	7 (A)				8 (A)				9 (Al)				10 (A)				11 (A)				12 (A)			
Nymphs born between day:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
0 - 7				1				2				4				6				5				4
8 - 18		1				1			5				4		1		4				5			
19 - 31	1.	1	1			1	1		1	3			1	2	1		2	2	1			2		
32 - 45	1				1					2				3				2				1		
Totals	2	2	1	1	1	2	1	2	6	5		4	5	5	2	6	6	4	1	5	5	3		4

Table 59b INDIVIDUAL PROGENY SEQUENCES OF VIRGINOPARAE TAKEN FROM SHORT DAY CONDITIONS AND PLACED IN LONG DAY CONDITIONS, AT 15°C

Number of parent:	1 (A)				2 (A)				3 (A)				4 (A)				5 (A)				6 (A)			
Nymphs born between day:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
0 - 7	2	1		3	1	2		3		1		2		2		4		1		3		2		2
8 - 18	4	3			4					4			1	5			5	3			4	2		
19 - 31	2	2			4				4				3				2				4			
31 - 45	4				5				6				4				4				5			
Totals	12	6		3	14	2		3	10	5		2	8	7		4	11	4		3	13	4		2

Number of parent:	7 (A)				8 (A)				9 (A)				10 (A)				11 (A)				12 (A)			
Nymphs born between day:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
0 - 7				3		2		4		3		3		3		1		2		2		2		4
8 - 18	2				1				1	1			2				2	2			1	1		
19 - 31	3				4				2				3				2				3			
31 - 45	1				5				3				2				4				2			
Totals	6			3	10	2		4	6	4		3	7	3		1	8	4		2	6	3		4

Table 60

INDIVIDUAL PROGENY SEQUENCES OF VIRGINOPARAE IN SHORT DAY CONDITIONS HAVING PREVIOUSLY BEEN TRANSFERRED FROM SHORT TO LONG (AT 10°C)

Number of parent:	1				2				3				4			
Nymphs born between day:	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov	Ap	Al	M	Ov
0 – 4	2				2	2			4				3			
4 – 10	4	9			4	4			6					3		
10 – 12			1		2						1			1		
12 – 14				2		2		1			3		1	1		
14 – 17				1				2			3		1			2
17 – 20				2				1			1					2
Totals	6	9	1	5	10	6		4	10		8		5	5		4

in the spring because they are not present at a time when the day length is short enough to induce this form. This is in contrast to D.platanoidis (Dixon, 1971 a) and E.tiliae (Dixon, 1972 a) both of which produce sexual forms at longer daylengths than P.alni. A similar occurrence to P.alni happens with another rarer sycamore aphid, Drepanosiphum acerinum (Walker) (Dixon, 1971 a). In this species embryos remain undetermined until the parent reaches the fourth instar and this does not occur in the spring until early May. The photoperiod at this time exceeds the critical length and thus oviparae are not produced. In species such as D.platanoidis E.tiliae and also B.brassicae (Bonnemaison, 1951) M.viciae (Lees, 1960) and A.pisum (Lamb and Pointing, 1972) the individuals hatching from overwintering eggs cannot readily be induced to give rise to sexual morphs. Later generations can more easily be induced, however. This phenomenon has been labelled 'facteur fondatrice' by Bonnemaison (1951) and 'interval timer' by Lees (1960). Due to the critical daylength in P.alni being shorter than these aphids it appears that in this aphid there is no need for such a timing mechanism. Elkhider (1979) reported the lack of an interval timer in M.dirhodum as sexual forms could be induced in early spring. However, this could not be confirmed due to the lack of fundatrices.

Fundatrices and their progeny were not reared in short day conditions, thus the presence or absence of an interval timer could not be confirmed in P.alni. However, experimental evidence does suggest that a timer system is lacking. Sexual morphs are produced at a certain time of the year, regardless of generation. Males occurred first, followed by oviparae. Generations which in the field do not produce oviparae readily did so under short day conditions in a controlled temperature room. (table 58). When sexuals are produced they do not occur after a fixed number of offspring such as with M.viciae (Lees, 1959) and A.pisum (kenten, 1955; Lamb and Pointing, 1975) or after a fixed passage of time such as R.padi (Dixon and Glen, 1971). Male production characteristically reached a peak and then subsided with more oviparae being produced. This in contrast to E.tiliae

where males once produced form a constant proportion of the population (Dixon,1972a) or D.platanoidis (Dixon, 1971e). In D.platanoidis, males were produced in the fourth generation and their appearance was not related to day length. Even under conditions of a relatively high temperature ($15^{o}C$) and long photoperiod males were produced in autumn synchronously with those in the field. Obviously an interval operates on male production and is insensitive to daylength. In P.alni no males or oviparae were ever recorded from seven successive generations at $10^{o}C$, $15^{o}C$ and $20^{o}C$ in long day conditions. Thus an interval timer which is time dependent does not occur. Sexuals are produced in response to a shortening photoperiod and it appears that males are produced between $13\frac{3}{4}$ hours and 13 hours daylength and oviparae below $13\frac{1}{2}$ hours. It could be argued that P.alni thus possesses an interval timer sensitive to daylength but as the photoperiod necessary to induce sexuals only occurs once during the life cycle of this aphid, in late summer, this is hardly applicable.

Although males are induced by a photoperiod between $13\frac{3}{4}$ and 13 hours they may appear in the field over a period during which photoperiod falls well below this. The explanation is similar to that described by Blackman (1975) for M.persicae. In the ontogeny of an apterous female, sensitivity to photoperiod starts in the embryo several days before birth, at about the same time as the first eggs mature in her ovarioles. Thus the first offspring in her progeny sequence are determined by the current environmental stimuli which act upon this maturing embryo. As the first determination of an embryo is sex (Lees,1966), the photoperiod at the time may induce male formation. Thus an apterous adult born in mid August and maturing in early September will produce males first as these were irreversibly determined in late August when the aptera was still a nymph. As day length shortens the aptera responds by producing oviparae in the sequence and these are born after the males (tables 52 and 53). Higher numbers of males tend to be produced by adults in September compared to August. It is likely

that this is due to the greater fecundity of their parents, as a result of better food quality later in the season. This causes the sex ratio to vary throughout the season, a phenomenon also noted for E.tiliae (Barlow and Dixon, 1980). Therefore in field populations the telescoping of generations during the summer ensures a gradual change over to sexual morph production, not an abrupt one as may be implied from a photoperiodic response. The process requires several generations for development and thus enables the alder aphid to exploit its host plant effectively in a manner similar to D.platanoidis (Dixon, 1971a). In autumn the tree provides a rich food source for the aphids. If only sexual morphs were produced at this time populations would not increase. However by responding gradually to short day conditions, advantage may be taken of this improved food quality and increase in numbers, sexual production and egg laying can continue over several generations.

The maternal switching mechanism of the mother appears to be very flexible. Within a week a mother can respond to the current environmental conditions and produce embryos accordingly. Lees (1963) found that in M.viciae the maternal photoperiodic process is initiated about 2 days before the birth of the apterous parent whereas her first embryos are determined as virginoparae or oviparae several days after her birth. The mother aphid is sensitive to photoperiod for at least 20 days in her ontogeny, this period extending throughout her larval life and into her reproductive life (Lees, 1973). It was observed that aphids could be switched from ovipara to virginopara production more readily than in the opposite direction, and suggested that this was due to an accumulative effect of long-day photoperiods. In P.alni, the change in morph production appears to be readily induced whichever the change in photoperiod. This is further evidence for the lack of a timing system and that sexual morph production is in response to current environmental stimuli.

An interesting feature of this aphid is its ability to produce apterous and alate virginoparae, males and oviparae all from one parent. Lees (1959) reported that M.viciae apterous virginoparae could produce four morphs but these did not appear to be produced from one individual. In this respect, P.alni is similar to M.euphorbiae (MacGillivray and Anderson, 1964) and possesses characteristics of a monoecious and heteroecious aphid. The alate virginoparae which are produced before males in P.alni were morphologically identical to the alate forms produced during the summer. These alates yielded males and oviparae exclusively. They may therefore be analogous to a sort of gynopara although gynoparae produce only oviparae in M.euphorbiae and other host-alternating species. It should be noted that M.euphorbiae is considered heteroecious but MacGillivray and Anderson recorded all morphs on a primary host (raspberry) and a secondary one (potato). In Britain it usually overwinters parthenogenetically (Blackman, 1974). P.alni is confined exclusively to alder and thus has no reason to produce gynoparae. It is possible that the alate production in P.alni occurs through a similar mechanism to that proposed by Blackman (1975) for M.persicae. When in continuing short day conditions such as occurs in the field, the oldest embryos within the mother gradually lose their capacity to develop into apterae. Either the effect is cumulative throughout embryonic development or the maternal determiner imparts an 'alatizing' or more likely a 'non-apterizing' stimulus (repressant) to the developing embryo until its birth. Thus the offspring produced after the apterae are irreversibly determined as alatae. Developmental pathways have been proposed for the various forms of aphids by Lees (1966). One such possible pathway describing the events in P.alni is illustrated in fig.143. This is related to the stage of embryonic development. It must be stressed that this pathway is hypothetical and would need rigourous experimentation to indicate its accuracy.

Steel and Lees (1977) reported that group 1 neurosecretory cells in the protocerebrum are required for virginopara production in long day conditions

Figure 143:

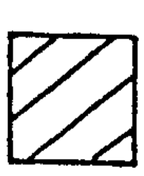
A hypothetical developmental pathway

for P.alni

Figure 144:

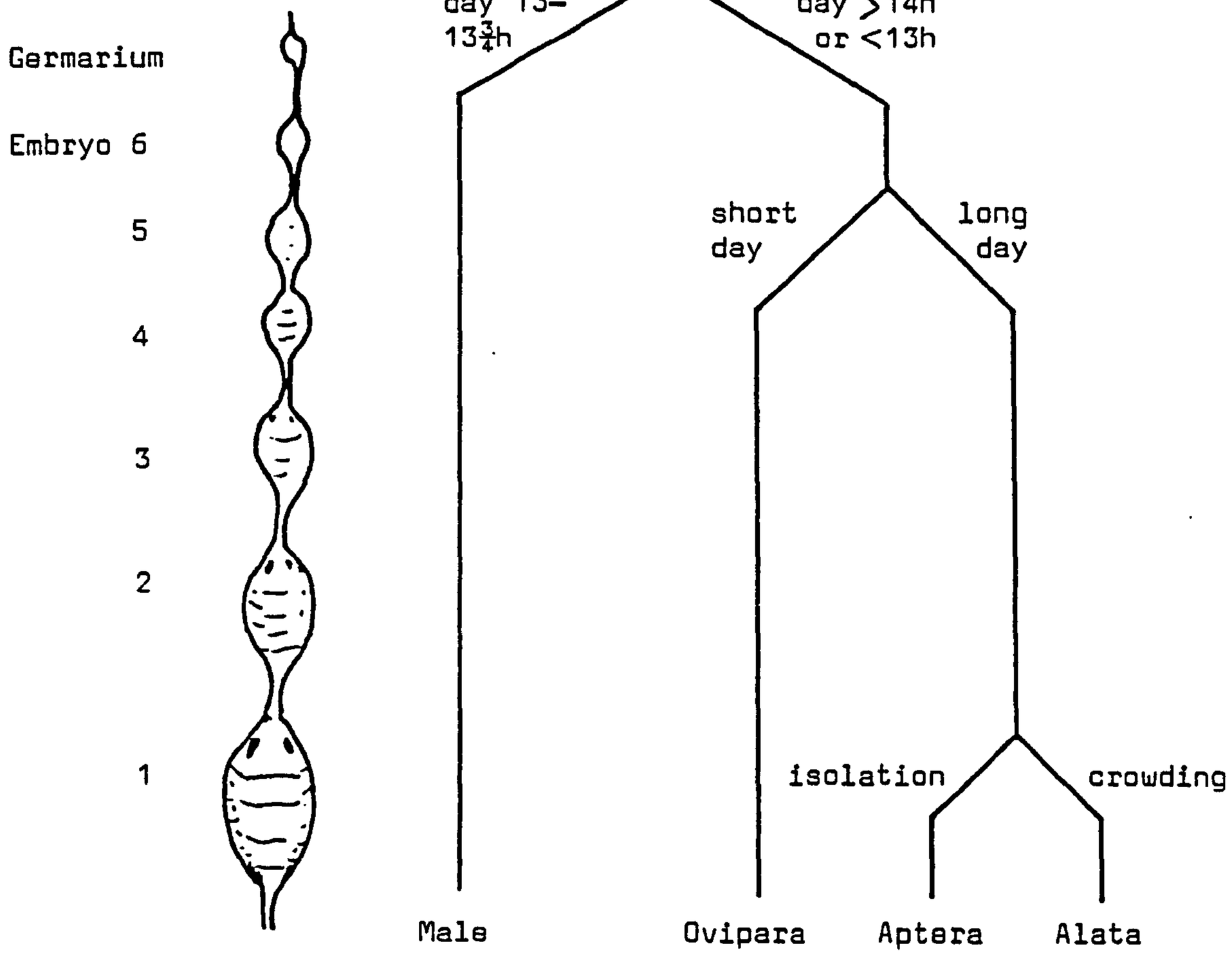
Design of box to measure egg laying by

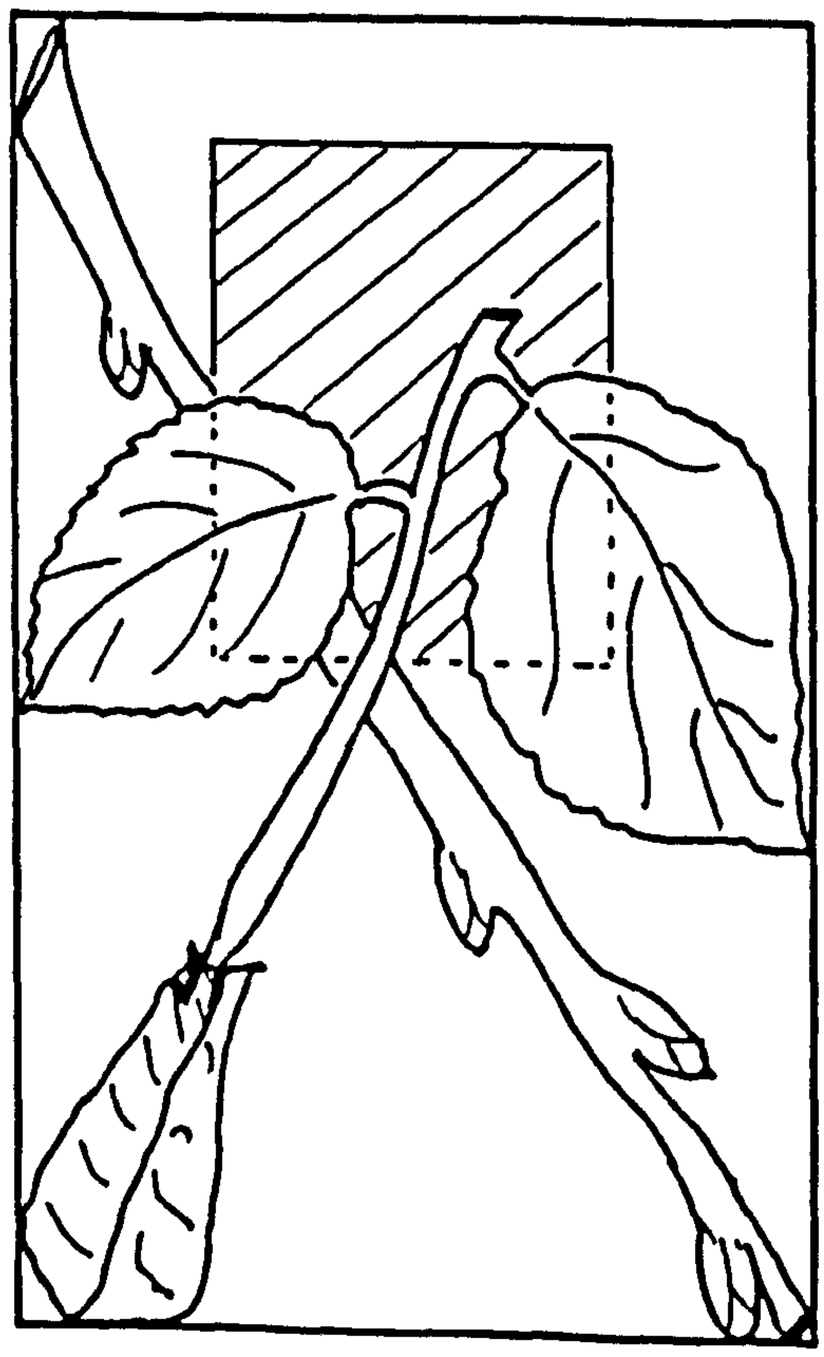
oviparae under controlled conditions



muslin'window' to allow

air flow


Germarium
Embryo 6
5
4
3
2
1
day 13–13¾h
day >14h or <13h
short day
long day
isolation
crowding
Male
Ovipara
Aptera
Alata



4 cm

but not for ovipara production in short days. These authors proposed that the role of these cells is in the maternal control of switching and that the development of the progeny, once determined by the mother as virginoparae or oviparae is under intrinsic endocrine control. Areas lateral to the group 1 cells are also required for the long-day response; thus the photoperiodic clock is probably located in this area. The clock regulates the release of neurosecretory material from the group 1 cells. This 'virginopara determinant' (Dixon 1985a) may be delivered directly to the embryos via the thoracic ganglion or released into the blood as a neurohormone. However, it has also been shown that juvenile hormone can mimic long-day photostimulation (Lees, 1978) and that this hormone can cause apterization of presumptive gynoparae of A.fabae (Hardie, 1980). Thus it appears that the photoperiodic receptor may transmit its effect through secretions of the corpus allatum, possibly under control of the group 1 cells (Hardie and Lees, 1983). If such a control system operates in P.alni it may thus act in an apterizing manner. When production of the hormone begins to cease, embryos are not diverted from the alata pathway and thus some alatae are produced before the sexuals. Johnson and Birks (1960) suggested that aphids start out on an alate course of development and are 'diverted' from it by conditions that are favourable to the production of apterous forms.

Throughout these experiments a wide range of reactions were observed between mothers and the offspring they produced. The most difficult factor to control when field experiments are undertaken is the amount of light received by an aphid feeding on the lower surface of a leaf. Such variations depending upon the position of a leaf on a branch may account for some of the differences. If, as suggested by Hardie (1984) that photoperiodically regulated polymorphism is controlled by a hormone such as juvenile hormone, then some variation may be due to differences within the mother of exposure of oocytes to the hormone or differing sensitivity to it. How chromosome behaviour is influenced by hormonal activity is still unclear, but Hales and

Mittler (1984) suggested that fluctuations in the level of circulating juvenile hormone could influence X-chromosome behaviour at or just before the (mitotic) maturation division of the oocyte.

The production of sexual morphs in response to changes in the food supply has been recorded only rarely. The subterranean Eriosoma pyricola Baker and Davidson cannot sense photoperiod directly but responds to seasonal changes in pear roots (Sethi and Svenson, 1967). Forrest (1970) observed that D.devecta responds to the cessation of shoot growth of apple trees. It is unknown what changes in the plant triggers the change in aphids but Harrewijn (1978) suggested a possible link between IAA and 5-hydroxytryptamine; a chemical which inhibits the production of winged offspring in M.persicae. Aphids with abbreviated life cycles occur and it appears that sexual forms are produced in response to the deterioration of the host plant. Such an aphid is M.abietinus on Frazer fir (Nettleton and Haine, 1982).

As sexual forms of P.alni were produced in the growth room where food quality was relatively stable (as plants originally had not been exposed to short day conditions) it is unlikely that host plant quality had an effect upon sexual morph production. Aphids were not reared upon actively senescing leaves in the field and all experiments took place on mature leaf tissue. Thus the role of the host plant is unlikely but cannot be eliminated due to lack of data. The host plant was shown to have no effect upon sexual morph production in D.platanoidis (Dixon,1971a) or E.tiliae (Dixon, 1972a).

Despite variation in results, the production of sexual morphs by P.alni has been examined in field and laboratory conditions. Much variation would be eliminated by rearing successive generations from egg hatch at constant temperatures and varying light regimes. In this way the response of the aphid to light/dark conditions and the critical photoperiod could be accurately determined.

4.2. OVERWINTERING OF P.ALNI - EGG PRODUCTION

4.2.1. Introduction

Oviparous females of P.alni posess a well developed sub-siphuncular wax gland field (Stroyan, 1977). Eggs when laid are yellow but soon darken to black. At the time of oviposition the egg is covered with white wax. Eggs may therefore be easily counted on branches in field and laboratory.

The weight and egg content of oviparae at maturity was examined and estimates obtained of eggs laid per ovipara in the field and under controlled conditions in the laboratory.

4.2.2. Materials and methods

Oviparae were reared on LF125 (A.glutinosa) at East Malling during late September and October, 1983. Two types of foliage were used: mature leaves on branches in the uncut section and young leaves which had been produced following pruning in July. Males were only reared on the mature foliage. Once adult, aphids were weighed on a Cahn 26 microbalance. The oviparae were subsequently dissected and the number of eggs counted. The stage of development of the eggs, the number of ovarioles and the number of eggs in each ovariole were recorded.

Samples of ten oviparae were placed in perspex containers on leaf tissue at 10°C, 15°C and 20°C. Two terminal leaves and a piece of twig to which these were attached were used. The cut end of the twig was wrapped in wet cotton wool and this covered in a piece of aluminium foil. Holes were bored in the back of the container and covered with netting to permit air flow and reduce condensation. One ovipara which had previously been observed to be mated was placed in each box together with a male.

Two pieces of twig from which the leaves had been removed and bearing four buds each were placed in the box to provide oviposition sites. The leaf tissue was changed at weekly intervals and the box, cotton wool, foil and twigs were examined and the eggs produced recorded. The arrangement is illustrated in fig.144. It was found that the method described above worked well at 10°C and 15°C but was impractical at 20°C. Leaves and oviparae died after two or three days. The experiment was discontinued at this temperature as it is very unlikely that oviparae would experience temperatures of 20°C for any length of time in the field.

Mated oviparae were released on to saplings of A.glutinosa, about 1.5 m high, in the University of London Botanic Garden, Egham, Surrey. These were left untouched until the last leaf had fallen. The saplings were then cut at ground level, taken into the laboratory and the eggs counted. Unfertilized eggs which had collapsed were also recorded.

4.2.3. Results

A total of 65 oviparae were reared on the mature foliage and 63 on the regrowth. These were born on September 23rd and became adult around October 22nd. The average weight of aphids reared on mature leaves was 0.498 mg with a 95% range from 0.486 mg to 0.509 mg. Those reared on the regrowth foliage weighed 0.309 mg (95% range: 0.289 mg-0.320 mg) and were thus significantly lighter at maturity ($d= 15.99$, $p<0.001$). A total of 56 males were reared and these weighed on average 0.150 mg (95% range: 0.149 mg-0.151 mg) at maturity. The males were considerably lighter than the oviparae reared on the similar foliage ($d= 28.69$, $p<0.001$).

When dissected, all oviparae were found to contain mature or virtually mature eggs of a deep yellow colour. The number of ovarioles was 8 in all aphids and no more than 3 eggs were ever found in an ovariole. The distribution

of the egg content of aphids reared on the mature leaves is depicted in fig.145. The mean number of eggs per aphid in this sample was 13.42 (95% range 12.7 - 14.2) with a modal value of 14. However, oviparae reared on the regrowth foliage contained an average of 5.54 eggs (95% range 4.9 - 6.2); a significantly smaller amount ($d=15.89$, $p<0.001$). Using the oviparae reared on mature foliage, there was a good relationship between egg content and ovipara weight, over the range of weights examined (fig.146a), ($r=0.737$, d.f. = 63, $p<0.001$). However, it is possible that the relationship may be curvilinear as egg content is unlikely to increase beyond a certain level, determined by the number present in the ovarioles. A plot of egg content against the logarithm of aphid weight gave a marginally better fit (fig.146b) with $r=0.747$ ($p<0.001$). Ovipara weight is thus a result of the number of eggs it contains and that all of these are matured soon after adulthood. This was further substantiated by dissecting oviparae found on the windbreak during October and November. No aphids were found with half-matured eggs and the egg content decreased as autumn advanced (fig.146c).

The egg laying patterns of oviparae at $10^{o}C$ and $15^{o}C$ are presented in fig.147 a,b. It can be seen that most of the eggs were laid within the first week after mating. At $10^{o}C$, 58% of the eggs laid were produced in the first week, whereas at $15^{o}C$ this figure was 88%; a significant difference ($d= 5.58$, $p<0.001$). Thus eggs were laid more quickly at the higher temperature, an obvious result of increased metabolism. There was no difference between the number of eggs produced at each temperature. At $10^{o}C$ the mean value was 14.2 eggs per ovipara and at $15^{o}C$ this was 13.7 ($t= 0.478$, d.f. = 18, $p>0.05$). Unmated oviparae showed very different patterns of egg laying. No eggs were laid at first and only a small number towards the end of the aphid's life (fig.147,c,d). The fact that the mean values of eggs laid were greater than the average previously determined may be explained by the fact that the oviparae used were larger than the mean

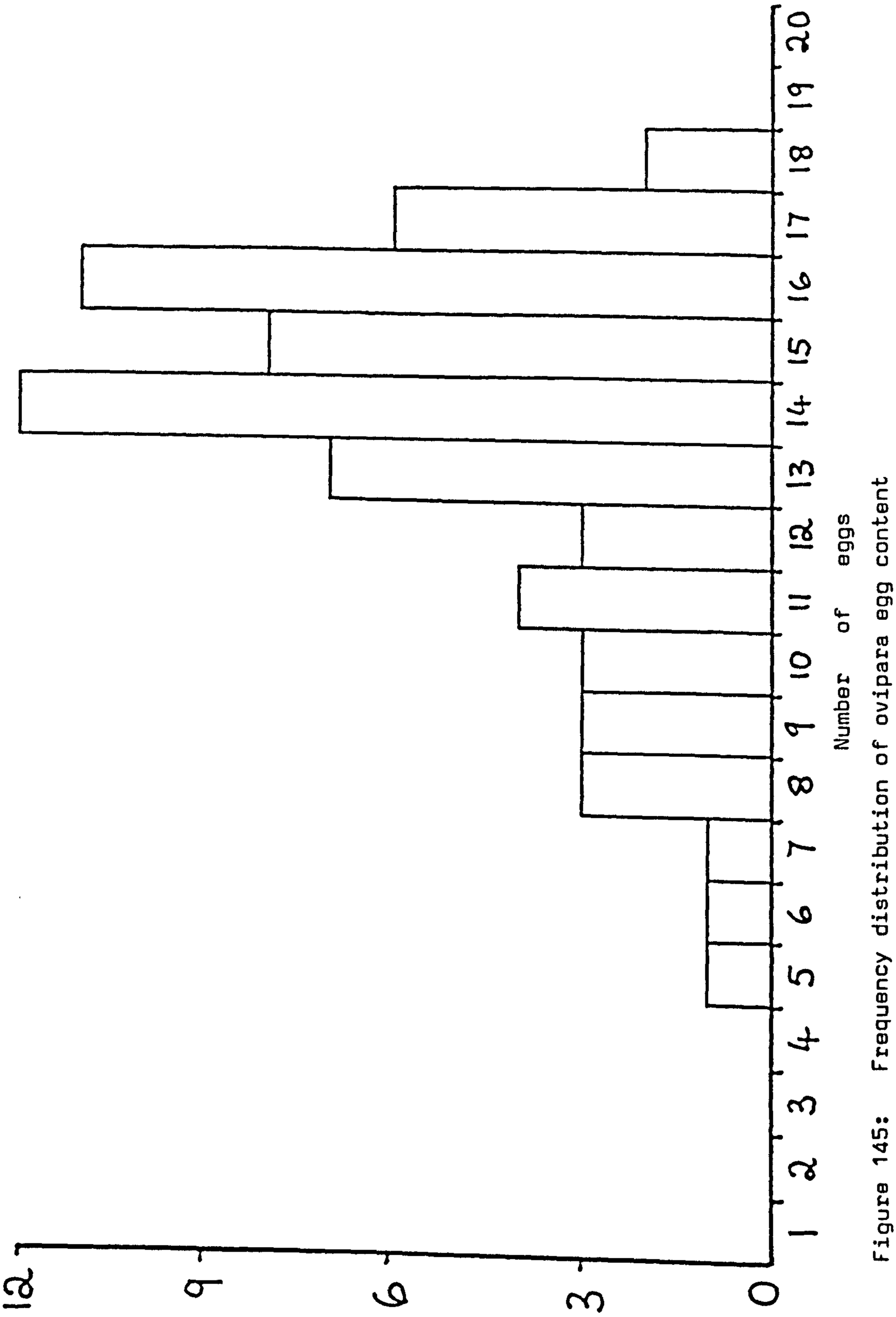


Figure 145: Frequency distribution of

Figure 146:

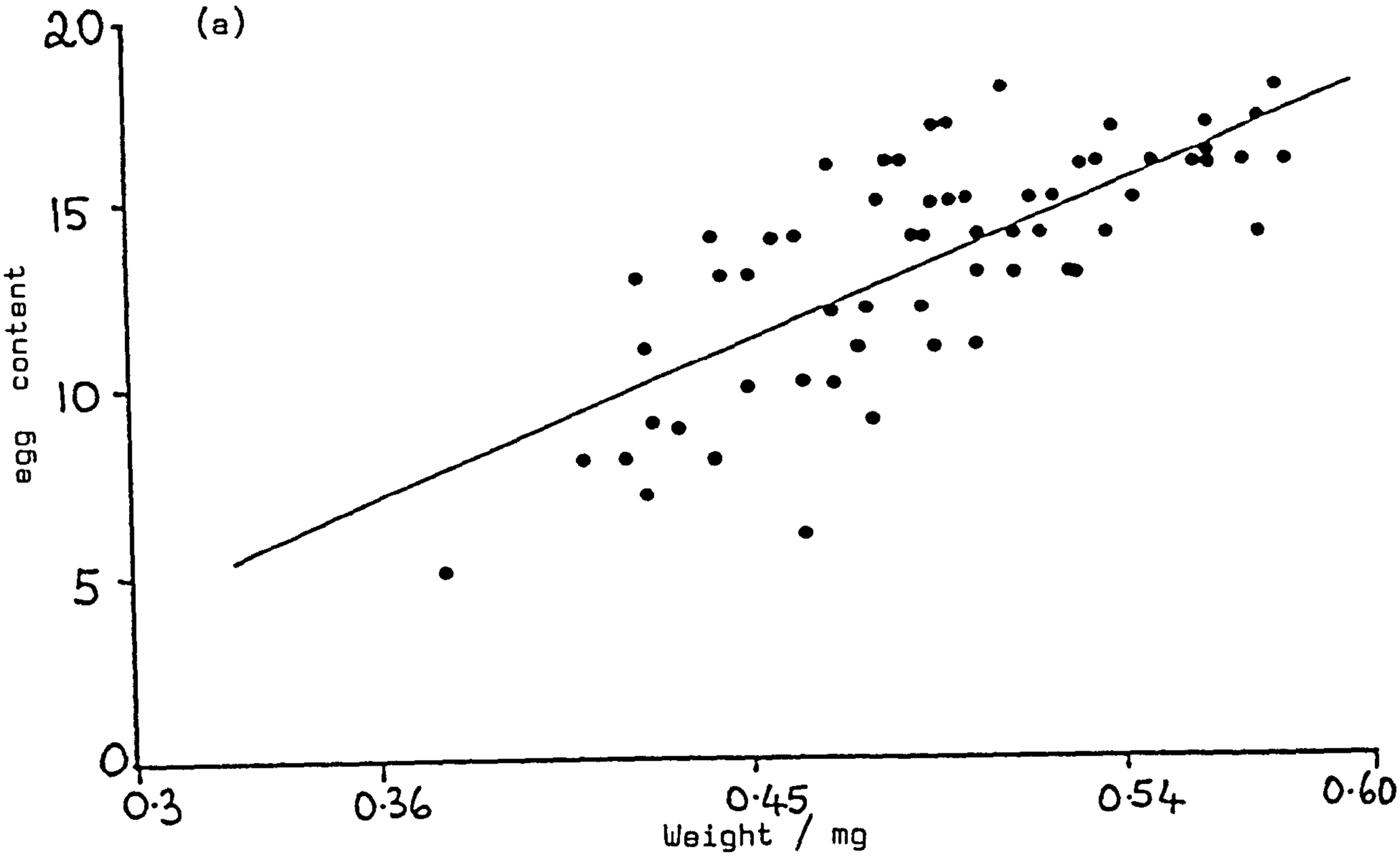
Egg content of oviparae

(a) Relationship between weight of an ovipara
and its egg content

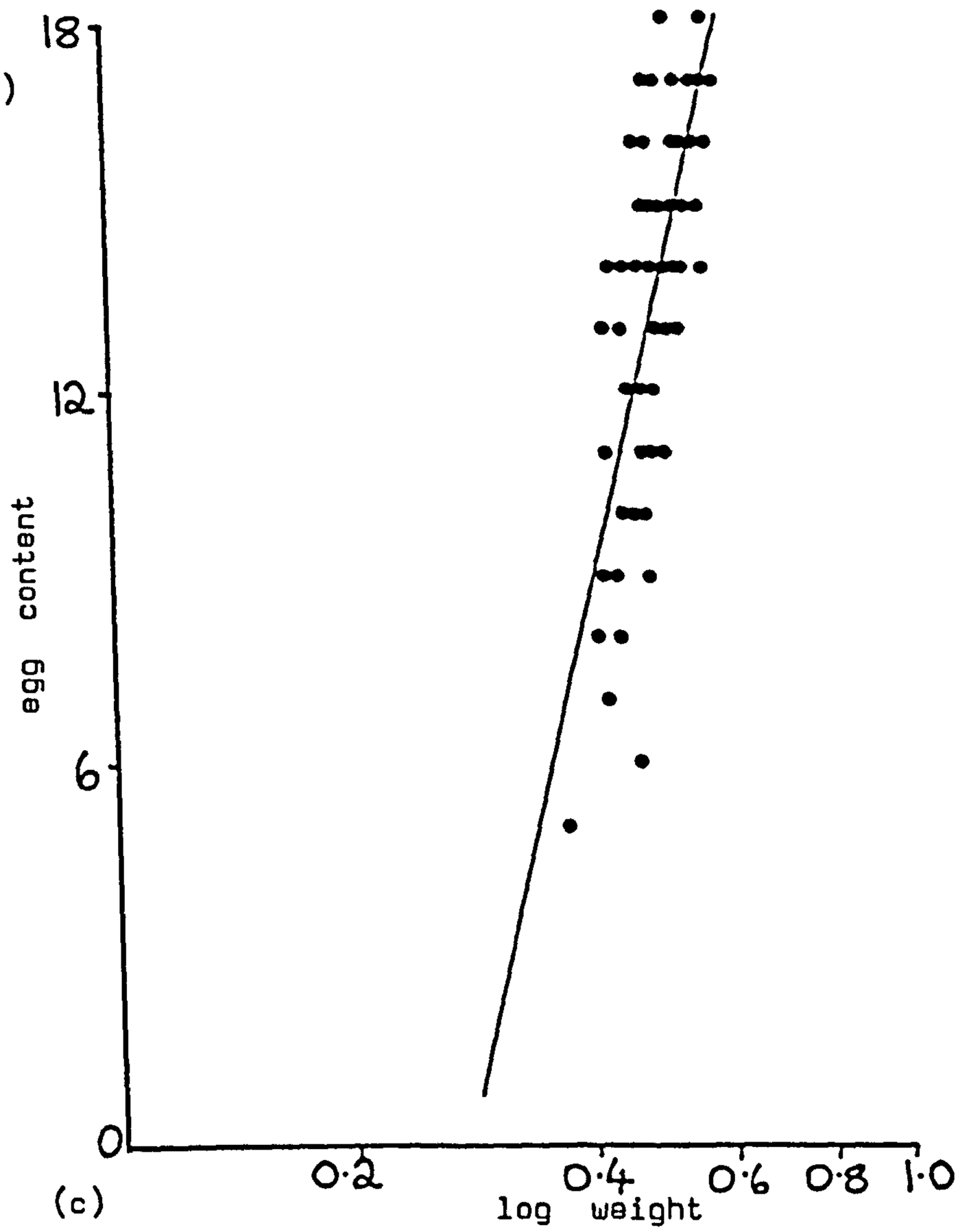
(b) Relationship between log weight and
egg content

(c) Mean egg content of oviparae found
on windbreak during autumn

(a)


20
15
10
5
0
egg content
0·3
0·36
0·45
0·54
0·60
Weight / mg

(b)


18
12
6
0
egg content
0·2
0·4
0·6
0·8
1·0
log weight

(c)

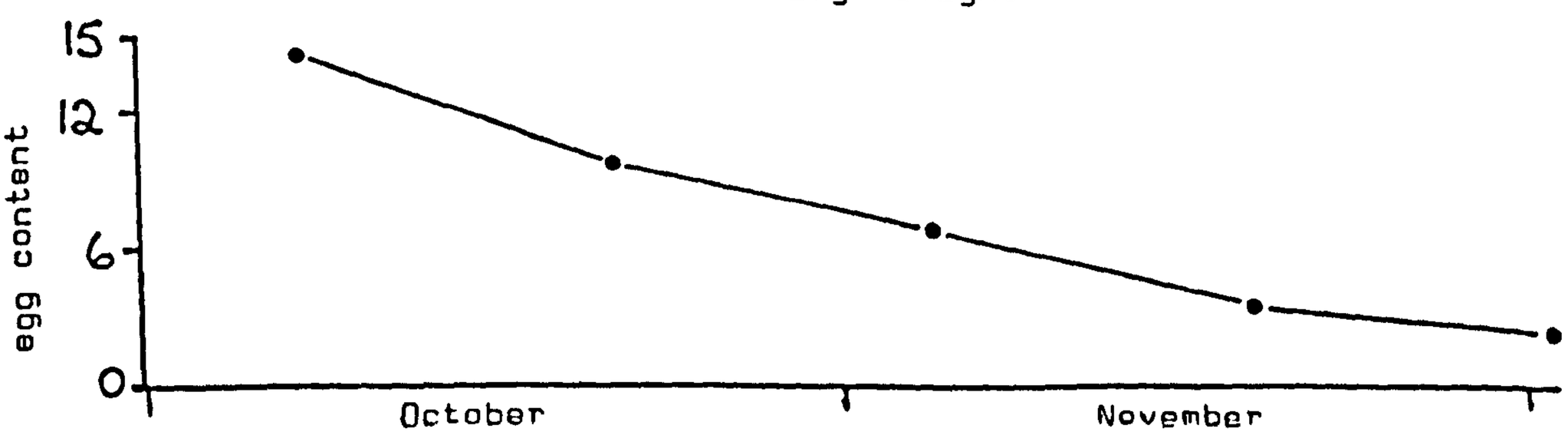

15
12
6
0
egg content
October
November

Figure 147:

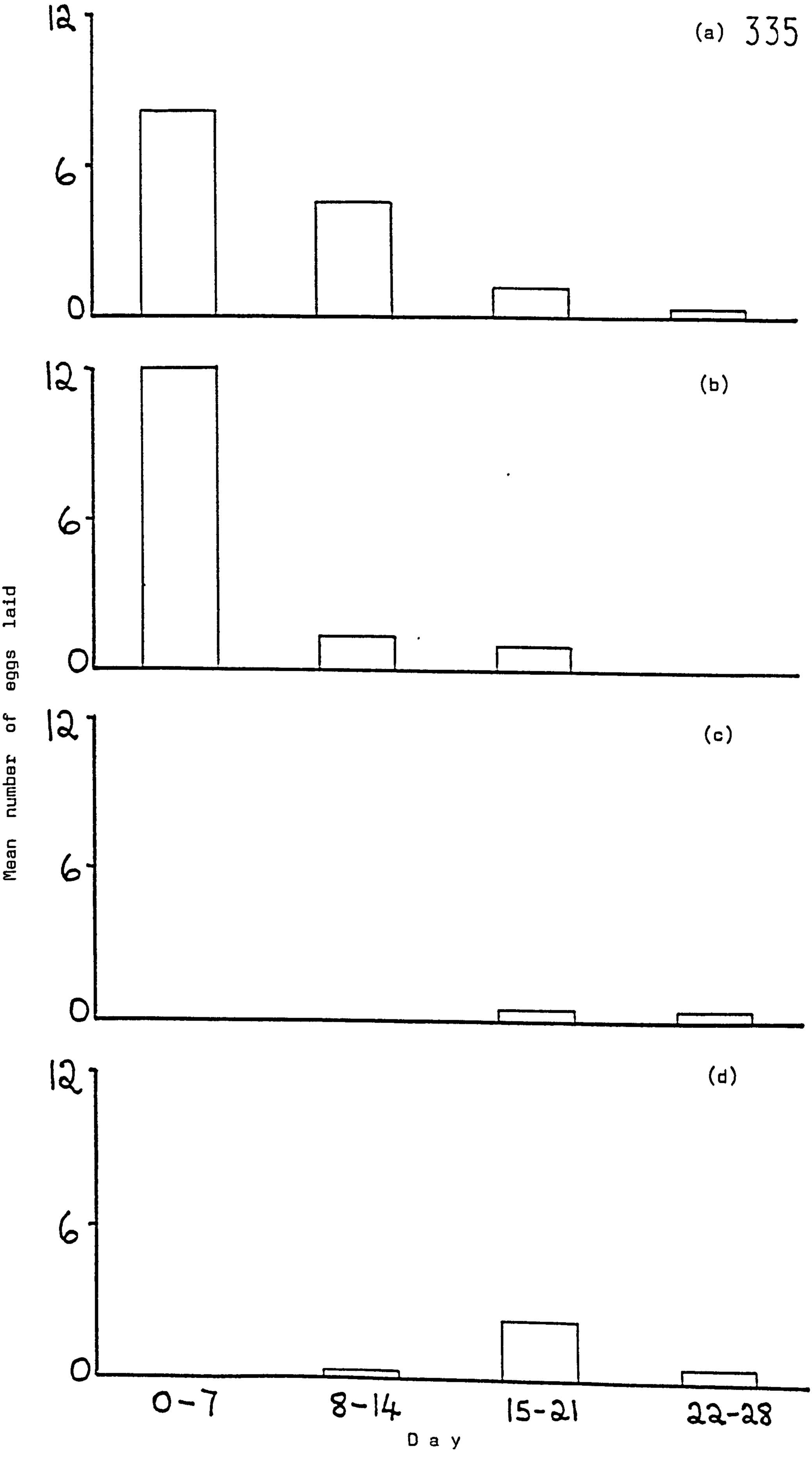
Egg laying by oviparae

(a) Mated, 10°C

(b) Mated, 15°C

(c) Unmated, 10°C

(d) Unmated, 15°C


(a) 335
(b)
(c)
(d)
12
6
0
Mean number of eggs laid
0-7
8-14
15-21
22-28
Day

calculated for the batch of 65. The mean weight of those used at 10°C was 0.525 mg (range:o.511-0.539) and at 15°C, o.518 mg (range 0.507mg-0.530 mg). By the relationship expressed in fig.146b, the aphids at 10°C contained 14.8 eggs at maturity and those at 15°C, 14.5 eggs. Thus it appears that under constant conditions virtually the full egg complement was laid.

At each temperature there was a strong relationship between the weight of the ovipara and the number of eggs it laid (10°C:r=0.792,d.f.=8,$p < 0.01$; 15°C:r=0.944,d.f.=8, $p < 0.001$), (fig.148a,b). Eggs were only found upon plant material, none were laid on the box,cotton wool or foil.

In the field a total of 90 oviparae were released on 10 saplings. The total number of eggs recorded was 531, an average of 5.9 eggs per ovipara. This is obviously considerably lower than the values obtained in a constant environment. It may be that this value underestimates the number of eggs produced in the field as predatory insects such as coccinellids or anthocorids may have attacked eggs during the period of oviposition. No attempt was made to exclude predators as the experiment was designed to simulate natural conditions where an ovipara is exposed to many mortality factors, including predation. A proportion of eggs found in this experiment had apparently collapsed. These were carefully examined, and those containing some liquid were considered unfertilized. Those which were empty were considered to have been attacked by predators. The piercing mouthparts of an anthocorid would allow the egg contents to be eaten without destroying the egg. It is not known whether the wax covering the egg would be a deterrent to anthocorids or coccinellids. A coccinellid might consume the entire egg.

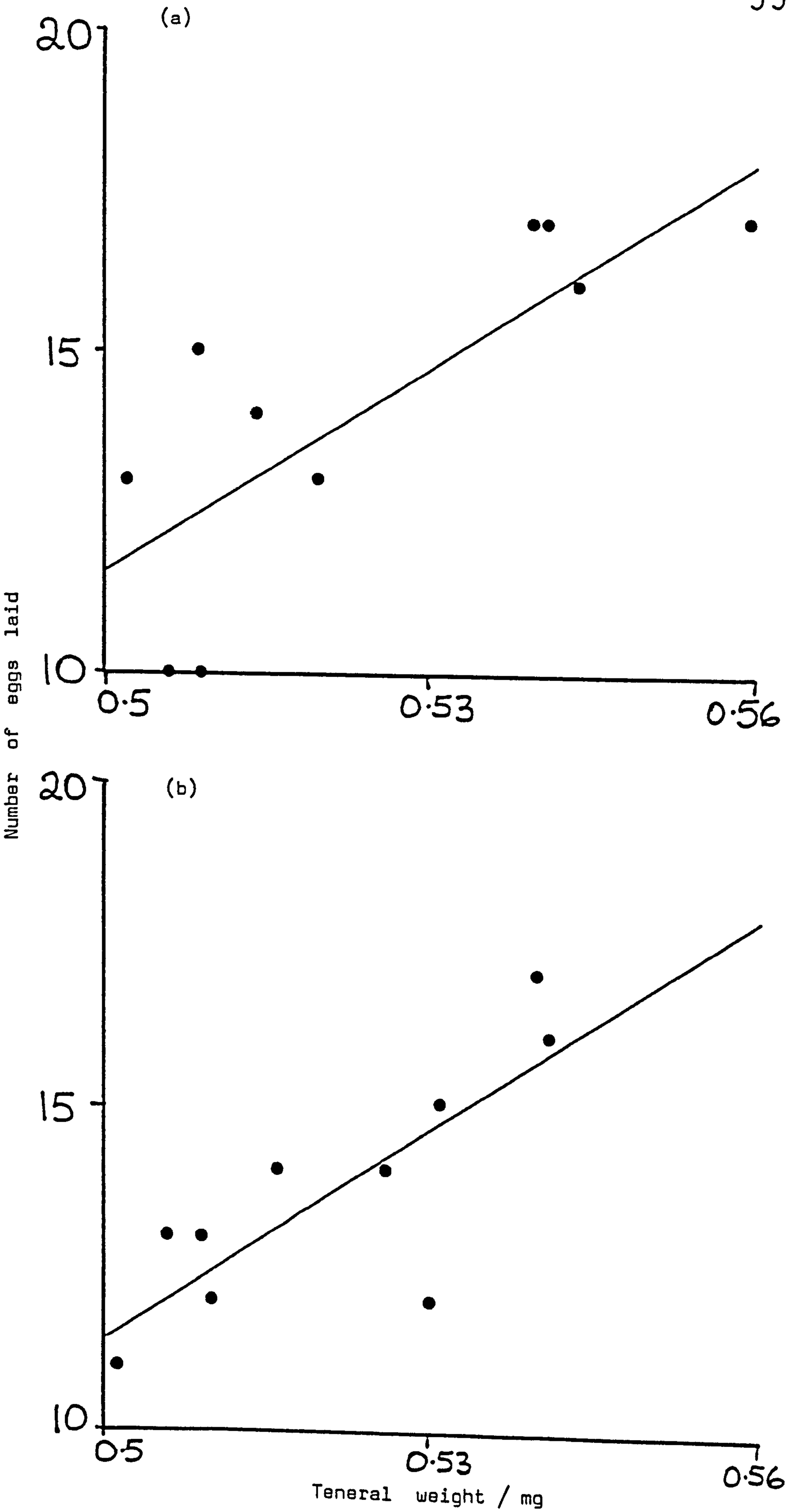
Of the 531 eggs, 64 were found to have collapsed and of these,55 contained liquid and 9 were empty. Thus 10.4% of eggs laid were unfertilized. No infertile eggs were found under constant temperatures. This may be due to

Figure 148:

Relationships between the teneral weight of an ovipara and the number of eggs it laid

(a) 10°C

(b) 15°C


(a)
20
15
10
0·5
0·53
0·56
(b)
20
15
10
0·5
0·53
0·56
Number of eggs laid
Teneral weight / mg

chance or the fact that some of the oviparae used in the field were not satisfactorily mated.

The finding that oviparae appear to mature all their eggs and then lay them quickly led to the possibility that they or the males may not feed. Oviparae were placed on leaves and clip caged. Circles of filter paper impregnated with bromocresol blue were placed in the bottom of the cage and the leaf arranged horizontally. Paper stained with bromocresol blue changes from yellow to blue when honeydew falls upon it (Banks and Macaulay, 1964). Thus the presence of blue spots would indicate feeding. The experiment was conducted in a constant temperature room at 15^{o}C to minimize the possibility of water affecting the paper as this also turns it blue. In all cases oviparae and males produced blue spots on the paper. Thus both sexes feed during their adult life.

Males were placed in perspex boxes with unmated oviparae. After several days the male was removed and placed with another unmated ovipara. The eggs produced by each ovipara were kept for a month and after this period their condition was noted as collapsed (unfertilized) or not. It was found that a male could fertilize more than one ovipara, one male fertilizing four before death. This may be a way in which males overcome their numerical disparity in the field.

4.3. OVIPOSITION

4.3.1. Introduction

Oviposition studies of aphids have in the past been used as a method for predicting subsequent outbreaks of pest species. A notable scheme has been that developed for A.fabae (Way, Cammell, Taylor and Woiwod, 1981). Studies upon the oviposition of aphids on trees are few and include that by

Dixon (1976a) on D.platanoidis and a detailed study by Cammell, Way and Heathcote (1978) concerning A.fabae on Spindle. This section reports on the oviposition of P.alni on A.glutinosa and the effect of winter pruning on egg numbers.

4.3.2. Materials and methods

Twenty-four branches were selected at random from the windbreak LF125 at East Malling in early November. The entire branch was cut from the tree at the trunk and taken into the laboratory for examination. Branches were removed from the western, unsampled face of the windbreak (fig.1). Twelve branches were removed from the pruned section (opposite the pruned sampled section) and twelve from a section which had not been pruned the previous summer. The windbreak is composed of a double line of trees and thus no branches were removed from trees whose leaves were sampled during the summer. All branches were of a similar size, with mean length 2.38m $\pm$ 0.07 m and presumably a similar age. Branches were cut into 10cm sections and examined for eggs using a x10 bench lens. The extent of the previous year's growth could be demarked by terminal bud scars and the fact that this 'first year growth' had bark which was greenish-brown in colour rather than that of the older wood which was grey. The older parts of the branches could not be aged. Egg positioning was recorded on the first year and older wood.

The alder branches characteristically consisted of the main branch, with side branches each of which bore twigs of first year growth. Buds were almost exclusively borne on these twigs. The length, number of buds and number of eggs was recorded for the complete twigs on the unpruned section.

Five branches were selected at random upon the windbreak. The number of buds and eggs upon them was counted three days before and after winter

pruning occurred, in late January.

4.3.3. Results

The oviposition sites recorded were (i) the axils of buds on first year or old wood (plate 3a), (ii) the axils between one year's growth and another or between two first year twigs (plate 3b), (iii) scar tissue formed where buds had broken off, (iv) crevices in the bark which began to form in the older wood (plate 3c) and (v) in the axils of the male catkin stalks. The distribution of eggs on the branches from each section is given in fig.149 a,b. On the uncut section 55% of eggs were laid on the first year wood compared with 47% on the cut section. This represented a significant difference ($d=2.69$, $p<0.01$) and reflects the fact that summer pruning removes a considerable proportion of first year growth but touches little of the older wood. Thus there were less oviposition sites available due to pruning.

On the first year wood of the uncut section, 87% of the eggs were laid in the bud axils (fig.149c), whilst on the cut section this figure was 90% (fig.149d); a similar proportion ($d=1.08$, $p>0.05$). Therefore, although there were less oviposition sites available on the cut wood, a similar proportion of eggs were laid in the bud axils. The choice of site thus remained the same. The majority of eggs laid on first year wood were in the bud axils. The only other site which appeared favourable were bud scars.

Although the egg numbers on the branches sampled varied from 10 to 169, the proportion laid upon the first year growth did not alter significantly (fig.150a:$r=0.156$, $d.f.=10$, $p>0.05$; fig.150b:$r=0.086$, $d.f.=10$, $p>0.05$). Thus it appears that counts of eggs on first year twigs can provide an adequate relative measure of the eggs laid on the windbreak.

PLATE 3

Oviposition sites of P.alni

(a) Bud axil, first year wood

(b) Twig axil, old wood

(c) Bark crevice, old wood

Figure 149:

Oviposition sites of P.alni

(a) Unpruned branches

(b) Summer pruned branches

Key: (1) Bud axil, first year wood
(2) Twig axil, " " "
(3) Bud scar, " " "
(4) Bark " " "
(5) Catkins " " "
(6) Bud axil, old wood
(7) Twig axil, " "
(8) Scar tissue " "
(9) Bark crevice" "

Figure 149:

Oviposition sites on first year wood

(c) Unpruned branches

(d) Summer pruned branches

Key: (1) Bud axil
(2) Twig axil
(3) Bud scar
(4) Bark
(5) Catkins

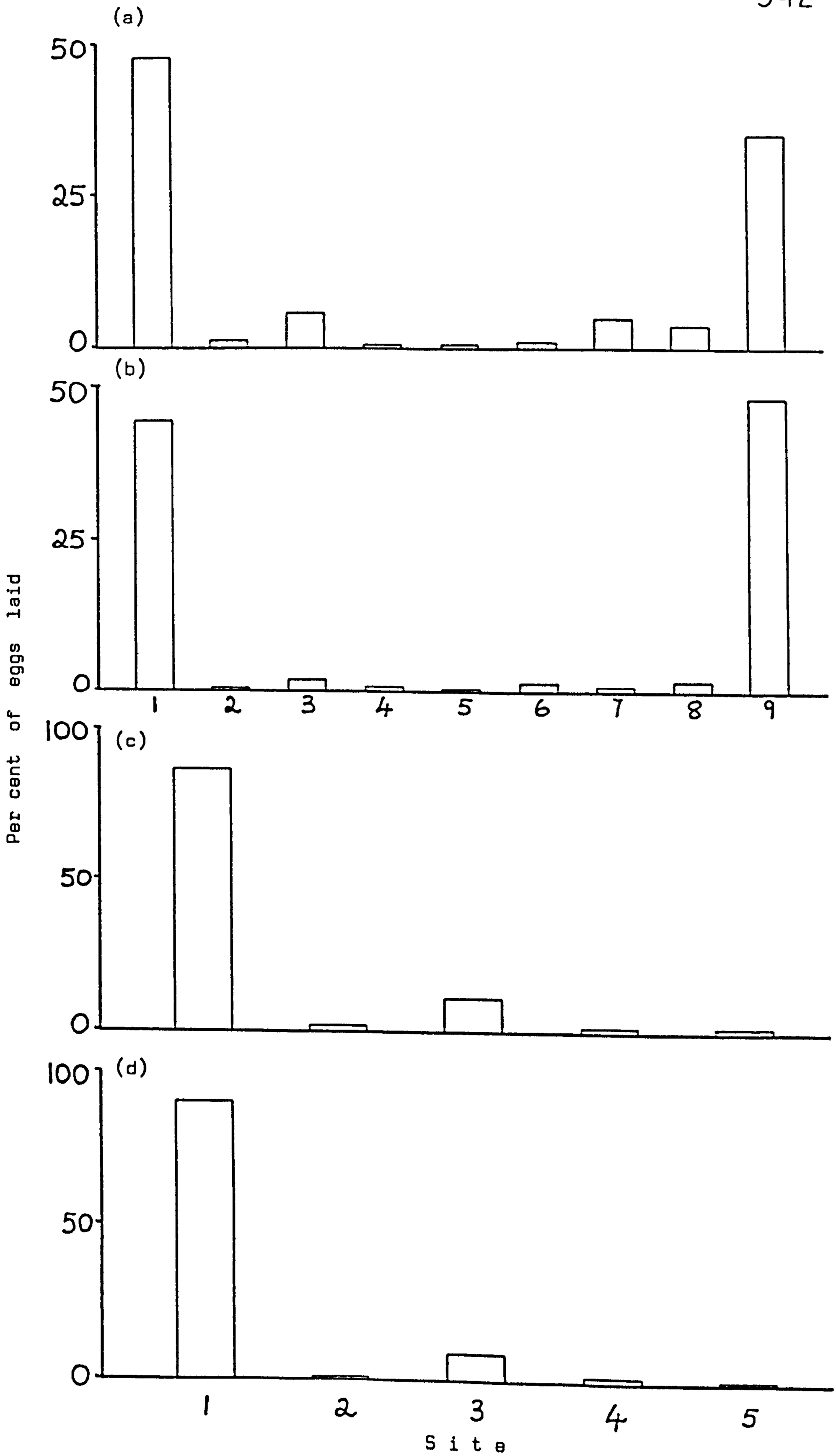

(a)
50
25
0
(b)
50
25
0
1
2
3
4
5
6
7
8
9
Per cent of eggs laid
100
(c)
50
0
100
(d)
50
0
1
2
3
4
5
Site

Figure 150:

The proportions of P.alni eggs laid on first year growth relative to the total numbers laid on the branch

(a) Unpruned

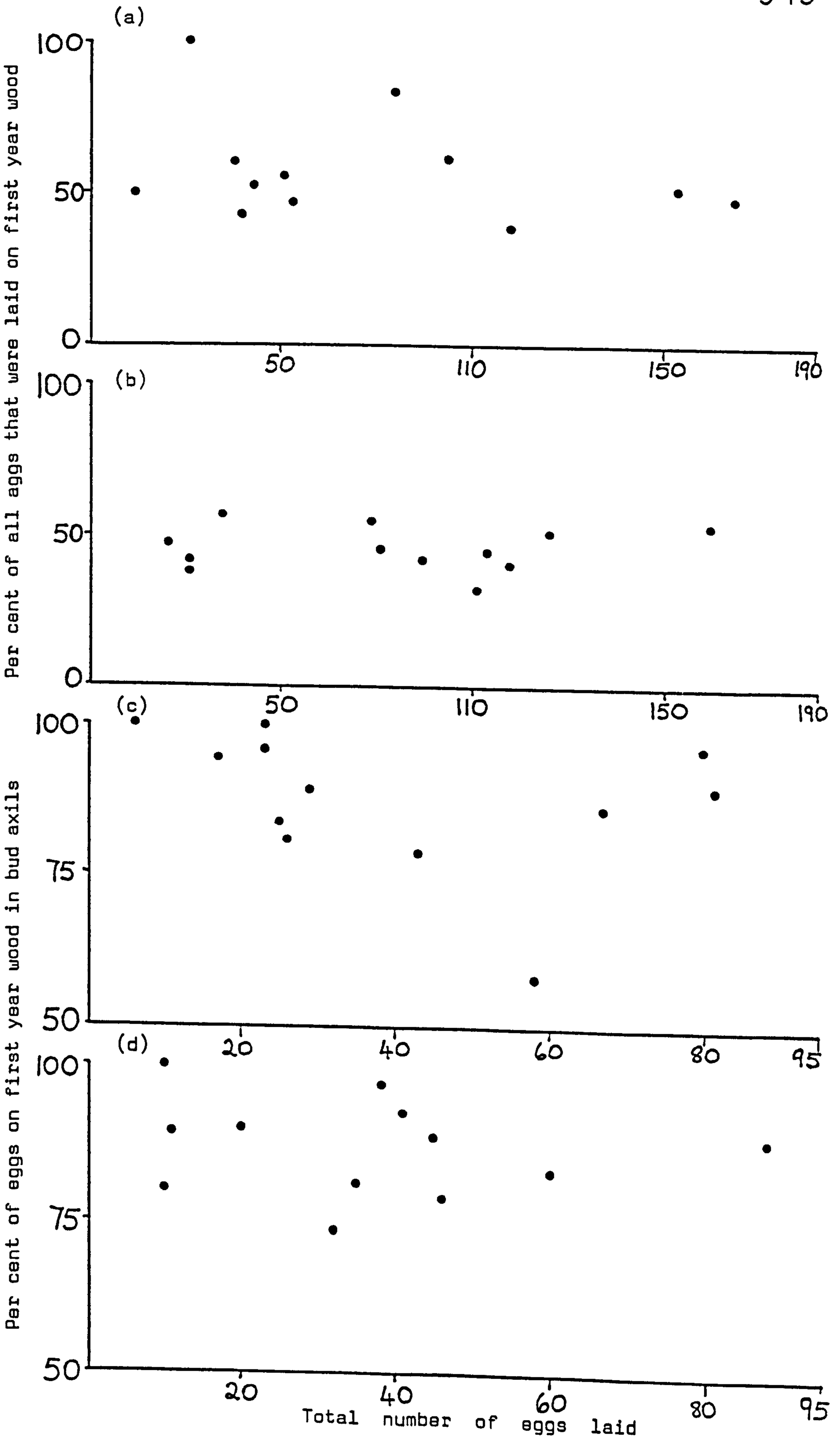
(b) Summer pruned

Figure 150:

The proportions of P.alni eggs laid in bud axils on first year growth relative to the total number laid on that wood

(c) Unpruned

(d) Summer pruned


(a)
100
50
0
50
110
150
190
(b)
100
50
0
(c)
50
110
150
190
100
75
50
(d)
20
40
60
80
95
100
75
50
20
40
60
80
95
Per cent of all eggs that were laid on first year wood
Per cent of all eggs that were laid on first year wood in bud axils
Per cent of eggs on first year wood in bud axils
Total number of eggs laid

The proportion of the eggs laid in the axils of the buds on the first year wood was not related to the total egg number upon that wood (fig.150c:r= -0.296,d.f.=10, $p>0.05$; fig.150d:r= -0.127, d.f.=10, $p>0.05$). Thus counts of eggs per bud on the first year growth can give a reliable estimate of egg abundance. The fact that sampling first year buds for eggs represents a constant proportion of the egg number meant that this method could be used for measuring egg abundance quickly throughout winter.

The uncut branches were divided into 10cm sections along the main 'stem' of the branch and the eggs within each section counted. These were expressed as number per unit area of bark. If a side branch emanated within a section, the egg count upon it was included in the relevant 10cm section. The distribution of eggs in relation to the mid point of each section is given in fig.151a, each point being the mean value for the twelve branches. Considering the whole branch, most eggs were laid in the middle section rather than at the terminal end or near the trunk. A likely explanation for this is that there were more side branches emanating from the main branch in the middle zone, thus providing more sites for oviposition (fig.151b). There was a good correlation between the eggs per cm^2 of bark and the number of side branches in each 10 cm. section ($r=0.767$,d.f.=22, $p<0.001$), supporting this suggestion. If the main 'stem' of the branch is examined, this too bore more eggs in the central sections (fig.151c). This is also a consequence of the number of side branches in the middle. Where these emanated from the branch, cracks and folds in the bark provided oviposition sites.

The number of eggs expressed per unit area of bark on each side branch bore no relation to the position of that sidebranch on the main branch (fig.152). Thus the side branches in the middle zone did not bear more eggs. The fact that there were more of them meant that more eggs were laid there.

Figure 151:

(a) Distribution of <u>P.alni</u> eggs

on alder main branches

(b) Distribution of side branches on

alder main branches

(c) Distribution of eggs on the main

'stem' of alder branches

(Curves fitted by eye)

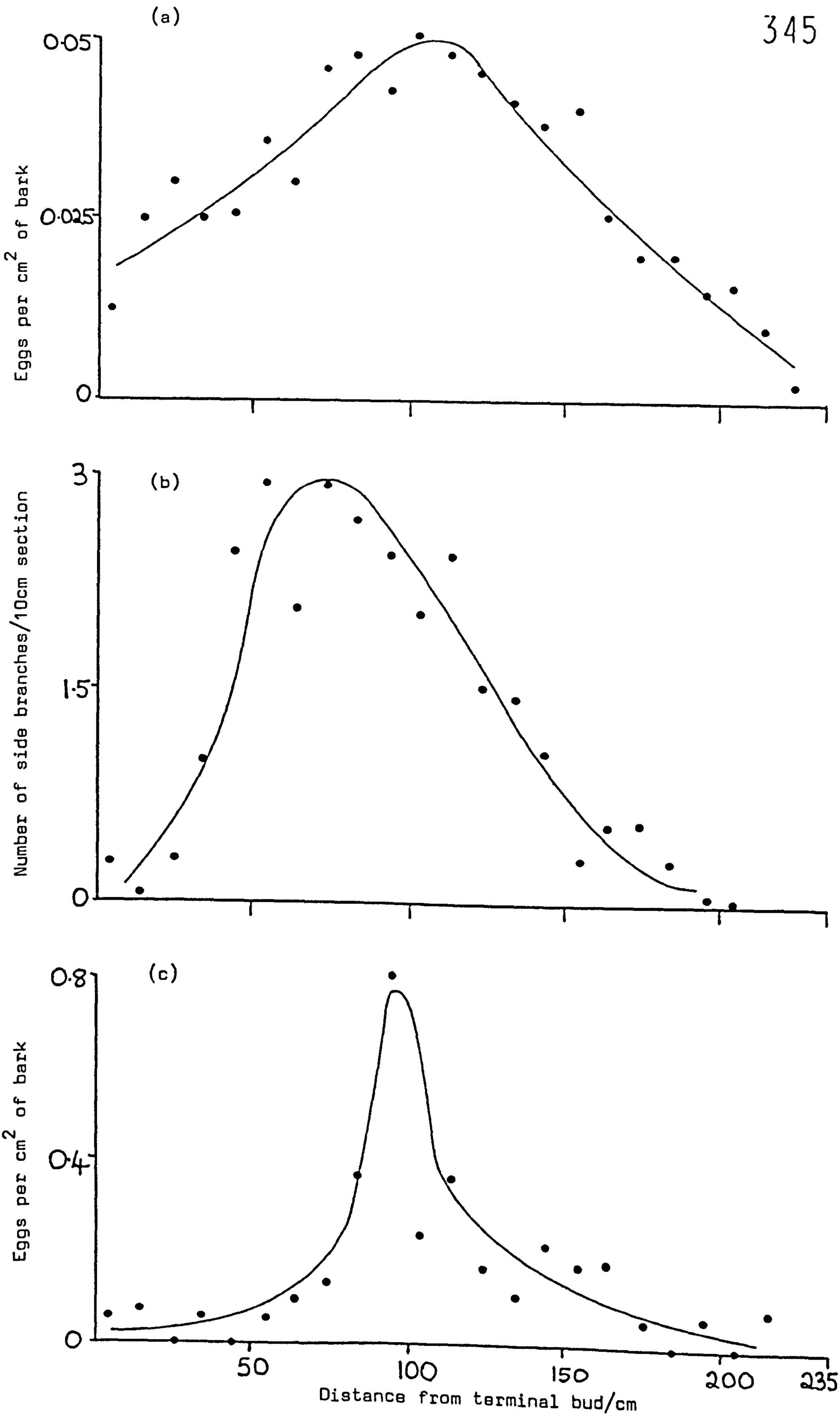
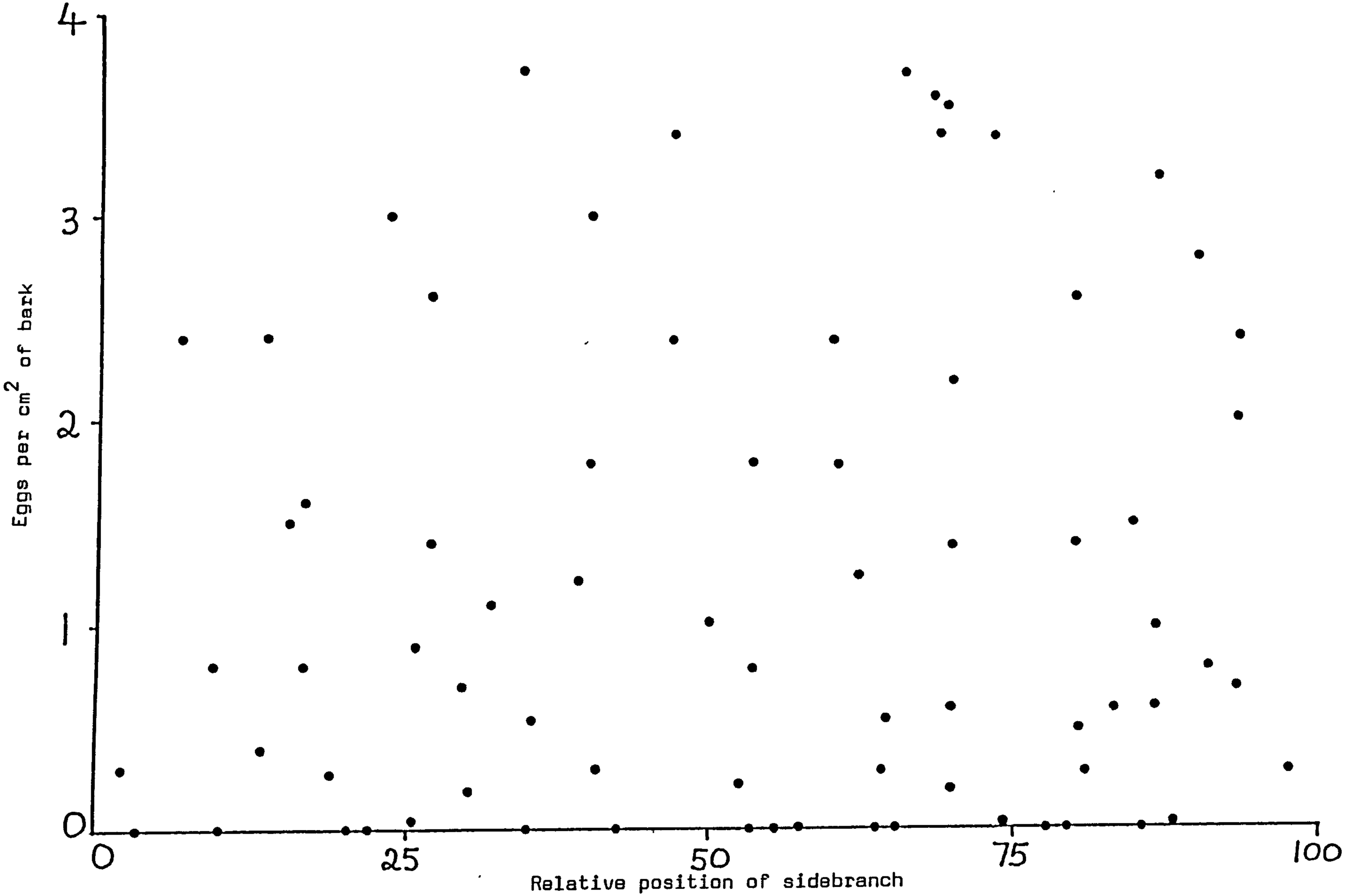

(a)
0·05
0·025
0
Eggs per cm² of bark
(b)
3
1·5
0
Number of side branches/10cm section
(c)
0·8
0·4
0
Eggs per cm² of bark
50
100
150
200
235
Distance from terminal bud/cm

Figure 152:

The abundance of eggs on sidebranches relative to the position of the sidebranch on the main branch

Relative position of sidebranch expressed as:

$$\frac{\text{distance from terminal bud}}{\text{main branch length}} \times 100$$


4
3
2
1
0
Eggs per cm^2 of bark
0
25
50
75
100
Relative position of sidebranch

There was a good relationship between the number of eggs on a first-year twig and its length (fig.153a, r=0.400, d.f.=96, $p<0.001$). This was largely a reflection of the increased number of buds on a long twig. The relationship between egg count and bud number was also highly significant (r=0.748,d.f.=96, $p<0.001$) (fig.153b). Using a z transformation the difference between these two values was significant (t=3.77,$p<0.001$). The better correlation between egg and bud number being due to the fact that eggs are laid in bud axils, not on the bark of the twigs.

The effect of pruning on the egg and bud numbers upon the branches was examined. The numbers before and after the treatment are given in table 61.

An average of 41% of the buds present on each branch were removed by the pruning process. The orientation of each branch in the windbreak differed, thus varying amounts of each were removed. Almost all of what was cut off was first year growth. As 55% of eggs are laid on this part of the branch and 41% of this was removed, it may be expected that 22.4% of the eggs would be lost. The observed removal was 25.3%, a significant difference ($d=2.00$, $p<0.05$). The fact that the observed loss was greater than expected could be due to inaccuracies in the methods used and that the proportions of eggs laid on the first year growth is not a true reflection of the egg distribution. A more likely explanation is that not only first year wood was removed in the pruning process, accounting for the 'extra' egg loss. Nevertheless, it appears that if a windbreak is pruned in winter 25% of the eggs present would be lost.

4.4. WINTER MORTALITY

4.4.1. Introduction

Aphid eggs suffer a characteristically heavy mortality during the winter

Figure 153:

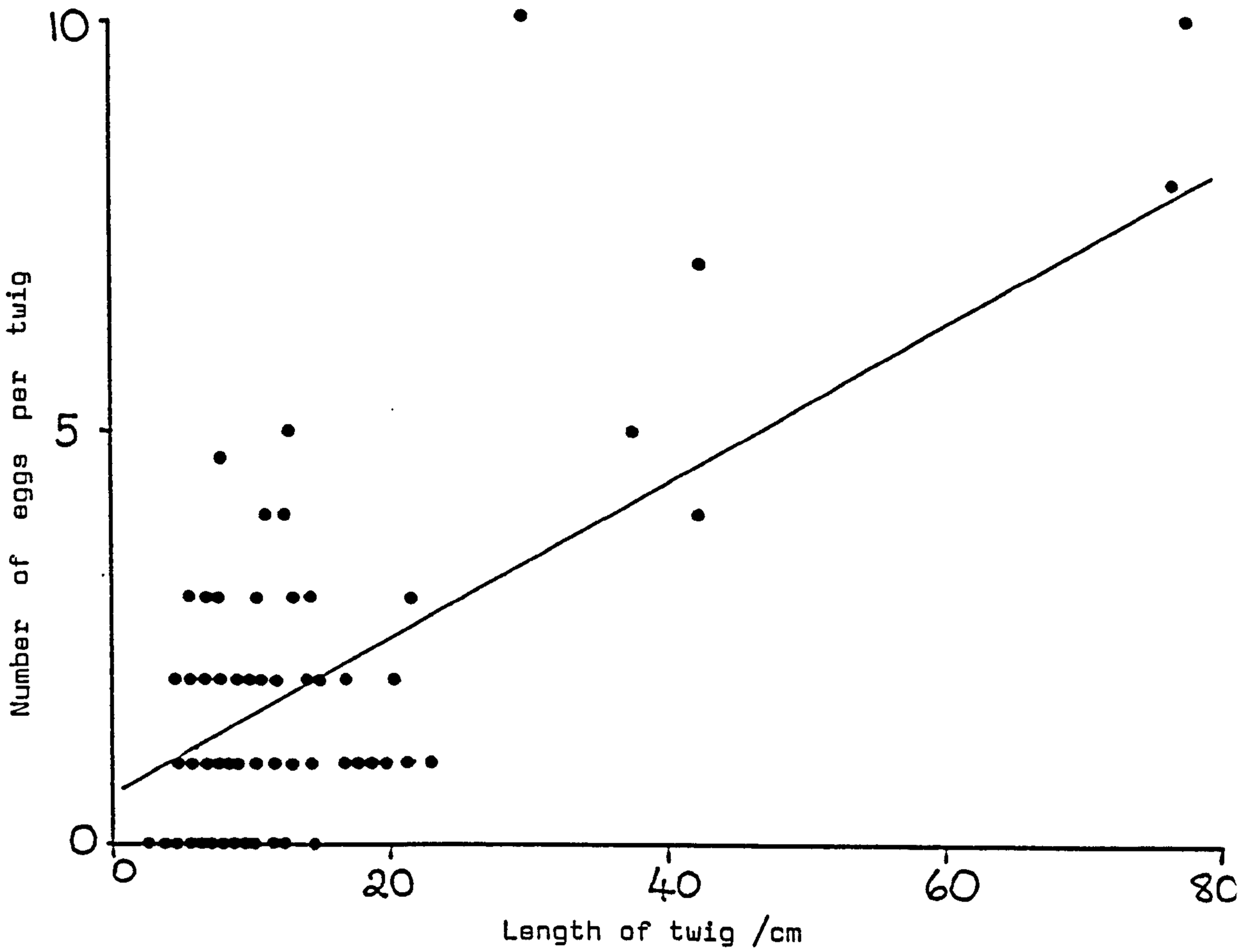
(a) The relationship between the length of the first year twigs and the number of *P.alni* eggs upon them

$$y = 0.09x + 0.61$$

(b) The relationship between the number of buds on a twig and the number of eggs on that twig

$$y = 0.65x - 0.94$$

(a)


10
5
0
Number of eggs per twig
0
20
40
60
80
Length of twig /cm

(b)

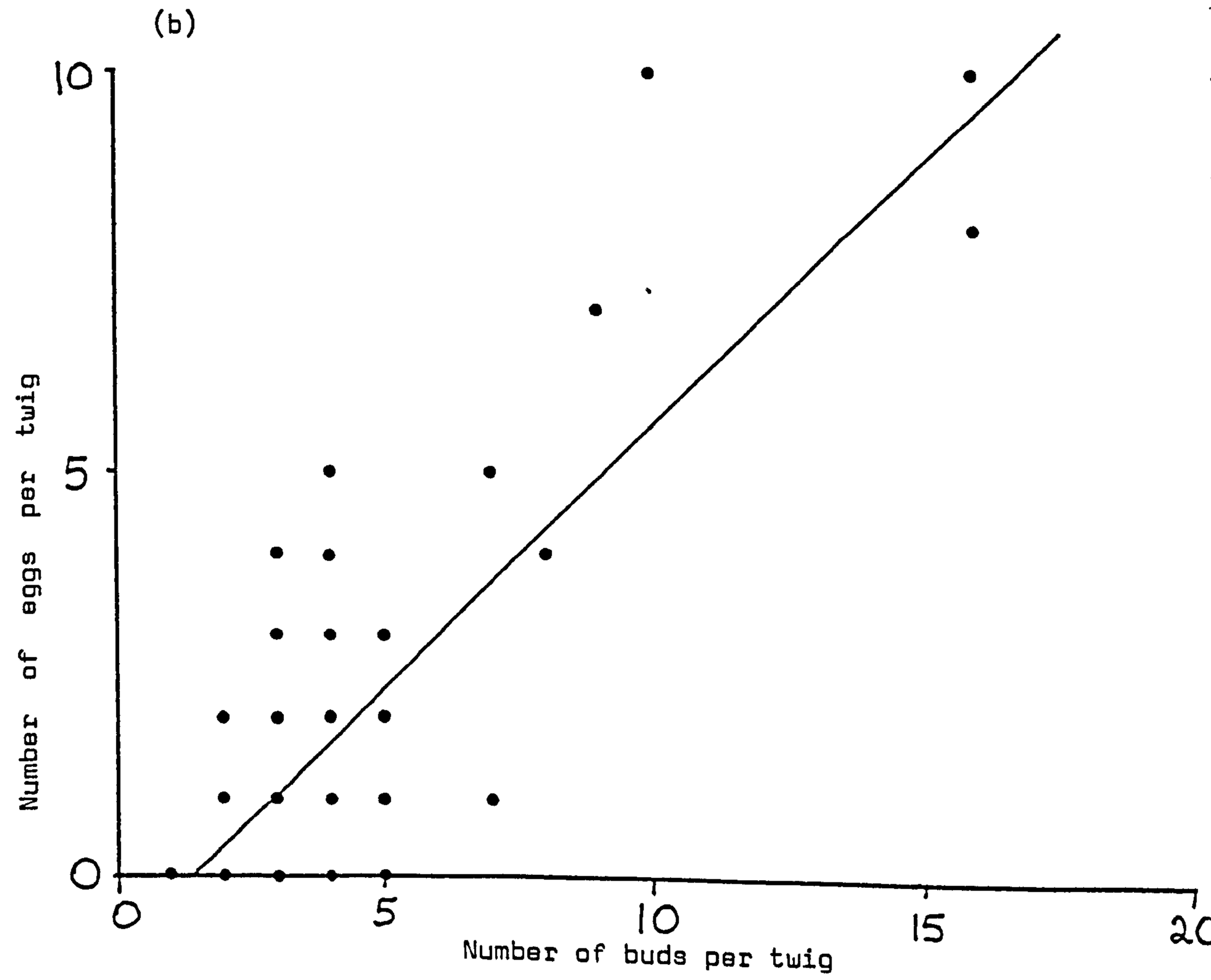

10
5
0
Number of eggs per twig
0
5
10
15
20
Number of buds per twig

Table 61 THE EFFECT OF WINTER PRUNING ON EGG AND BUD NUMBERS ON THE WINDBREAK

Branch	Number of eggs before pruning	Number of eggs after pruning	% removed	Number of buds before pruning	Number of buds after pruning	% removed
1	189	132	30.1	284	160	43.6
2	396	311	21.5	511	344	32.6
3	82	58	29.3	216	98	54.6
4	16	12	25.0	113	66	41.6
5	151	119	21.2	257	175	31.9
Mean (Arc sine transformed)			25.3			40.74

months. Some typical values reported are 70-80% for R.padi (Leather, 1980;1981), 83% for A.pisum (Dunn and Wright,1955) and 71-90% for Schizolachnus piniradiate Davidson (Kulman,1967). An exception is A.fabae of which the average mortality is considered to be 40% (Way and Banks,1964), although the range in that study was from 18 to 73%.

The majority of egg mortality has been attributed to insect and bird predation (Way and Banks, 1964; Leather,1981) although the effect of rain, through dislodging eggs and promoting fungal infection has also been considered (Dunn and Wright, 1955).

In this section the mortality of eggs in P.alni is investigated throughout the winter using the bud sampling technique, suggested in the previous section. Some of the causes of egg mortality were examined by predator exclusion experiments.

4.4.2. Materials and methods

The first year twigs bearing buds were sampled as examining these represents a constant proportion of the eggs on the windbreak (fig.150). Twigs were examined at random until 500 buds had been searched. The egg count was expressed as eggs/100 buds following the procedure of Leather and Lehti (1981). Samples were taken at least fortnightly from the end of September until April when egg hatch was followed at four-day intervals.

To examine some of the possible causes of egg mortality, branches were randomly selected upon the windbreak. Three branches were enclosed in cages built of chicken wire and 'weldmesh' in order to exclude birds. The eggs upon each branch were counted in late October 1983 and the cage then applied. Three branches were enclosed in the same manner, but in addition black 'insect and parasite proof' nylon netting (Watkins and Doncaster Ltd.,

Hawkhurst) was securely fastened over the cage in an attempt to exclude arthropod predators as well. Five branches were left uncaged throughout the winter of 1983-4. The eggs upon the uncaged branches were counted on the same days as when the buds were sampled.

4.4.3. Results

The numbers of eggs per 100 buds throughout the winters of 1982-'83, '83-'84 and from September 1984 until January 1985 for windbreak LF125 are given in fig.154 a,b,c.

The numbers of eggs upon the buds rapidly increased during the autumn as the oviparae were laying. This reached a peak in late November coinciding with the disappearance of oviparae and leaf fall. Thereafter the egg count fell sharply during December and January and levelled out to be fairly constant during February and March.

The proportion of eggs remaining after the peak count in each year followed a similar decline (fig.155 a,b). In each year there was a linear relationship between the number of eggs surviving and the time in weeks from the peak number of eggs recorded (fig.154). In 1982-83 this was $y = -1.79x + 62.5$ ($r = -0.839$, d.f.=9, $p < 0.01$) and 1983-84, $y = -1.28x + 37.5$ ($r = -0.907$, d.f.=9, $p < 0.001$). Egg mortality thus showed a constant rate throughout winter of 2.9% per week in 1982-83 amd 3.4% per week in 1983-84.

The number of eggs remaining on the uncaged branches throughout the winter is given in fig.156a and the proportion remaining in 156b. These graphs are very similar in form to those depicting egg loss by bud sampling and the linear relationship between the proportion surviving was also remarkably similar. For bud samples, the relationship between the proportion of eggs remaining (y) and the time in weeks from the peak egg count (x) was

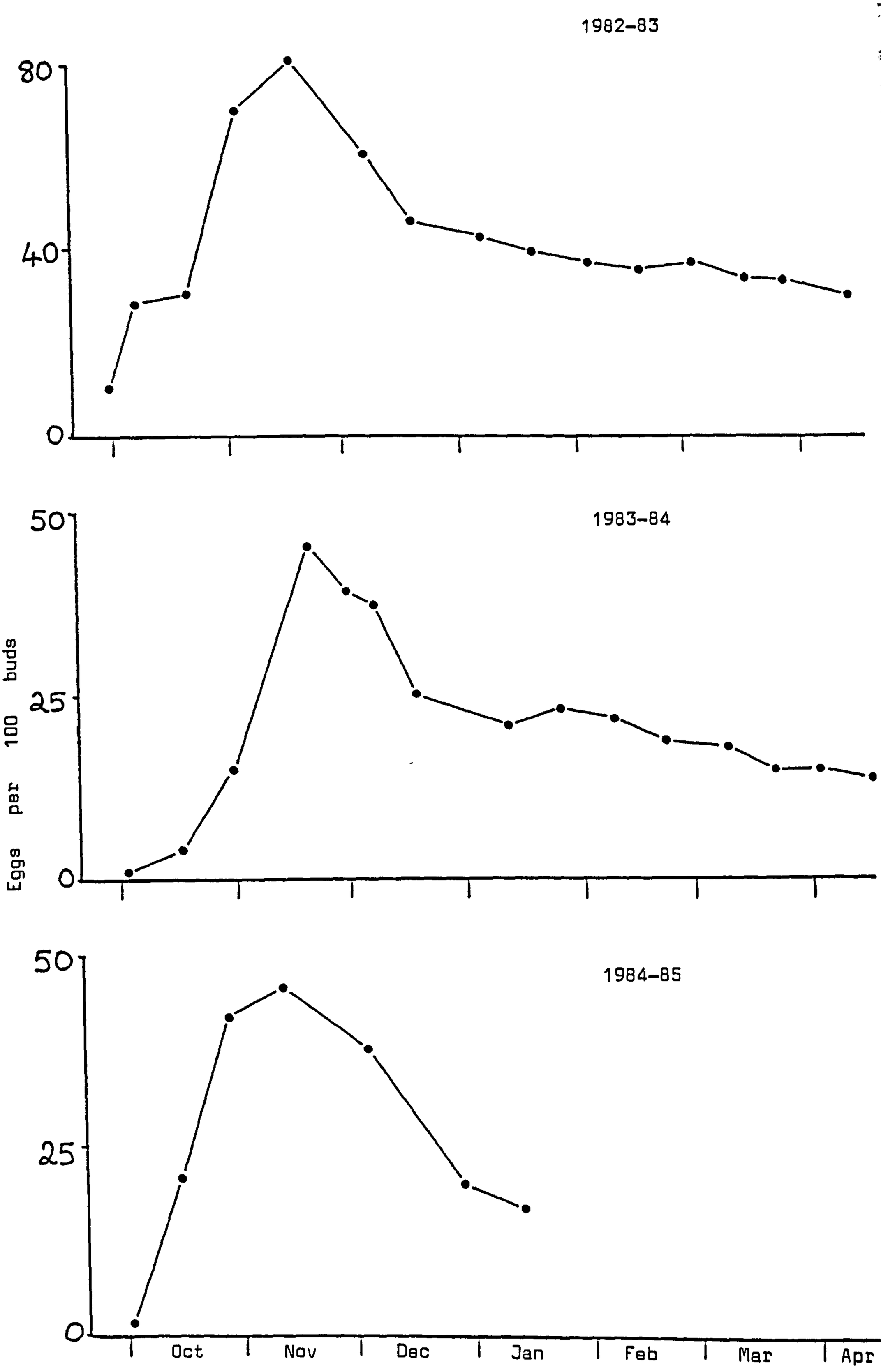


Figure 154: Abundance of eggs of P.alni on LF 125, measured by bud sampling

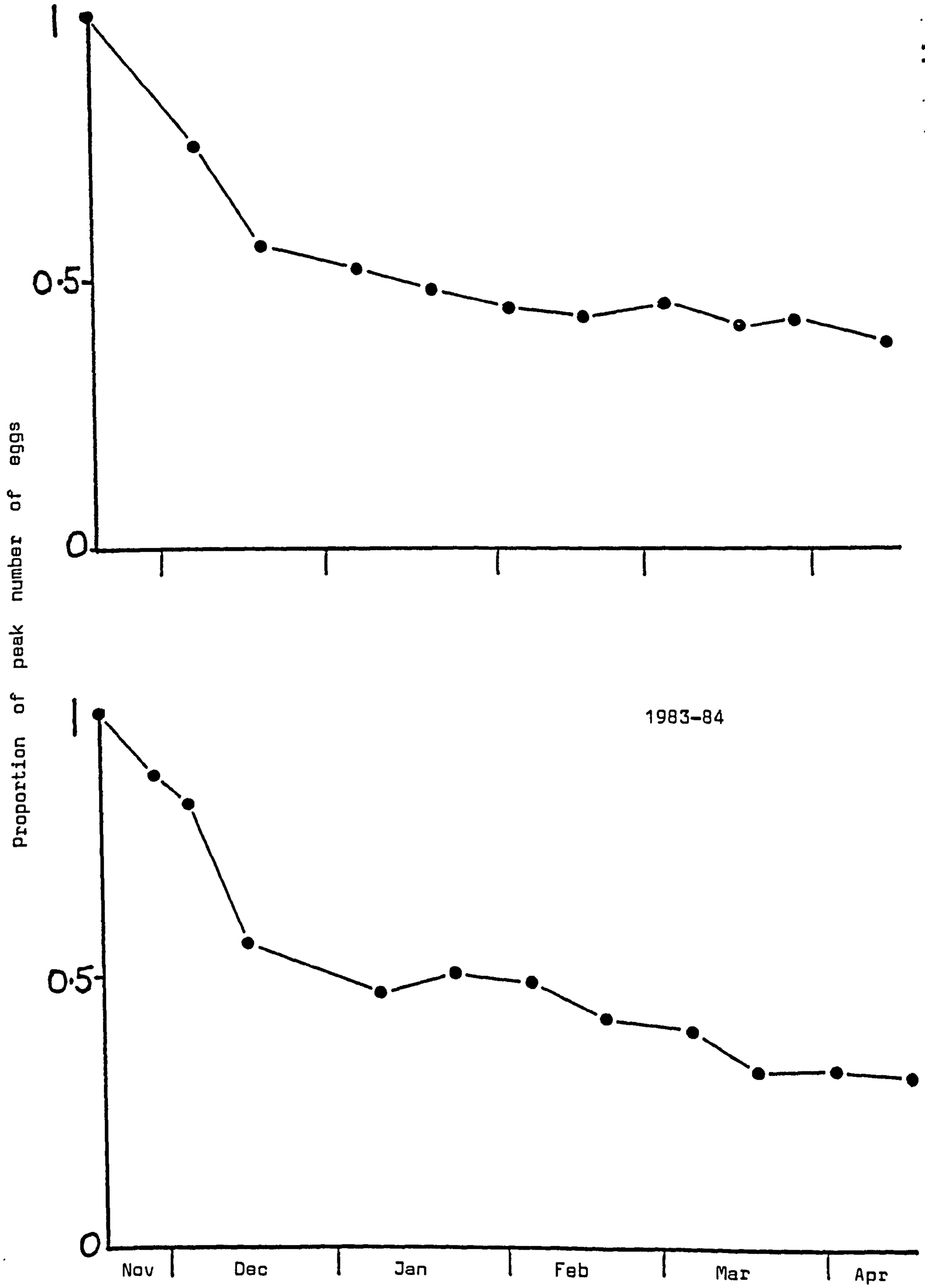
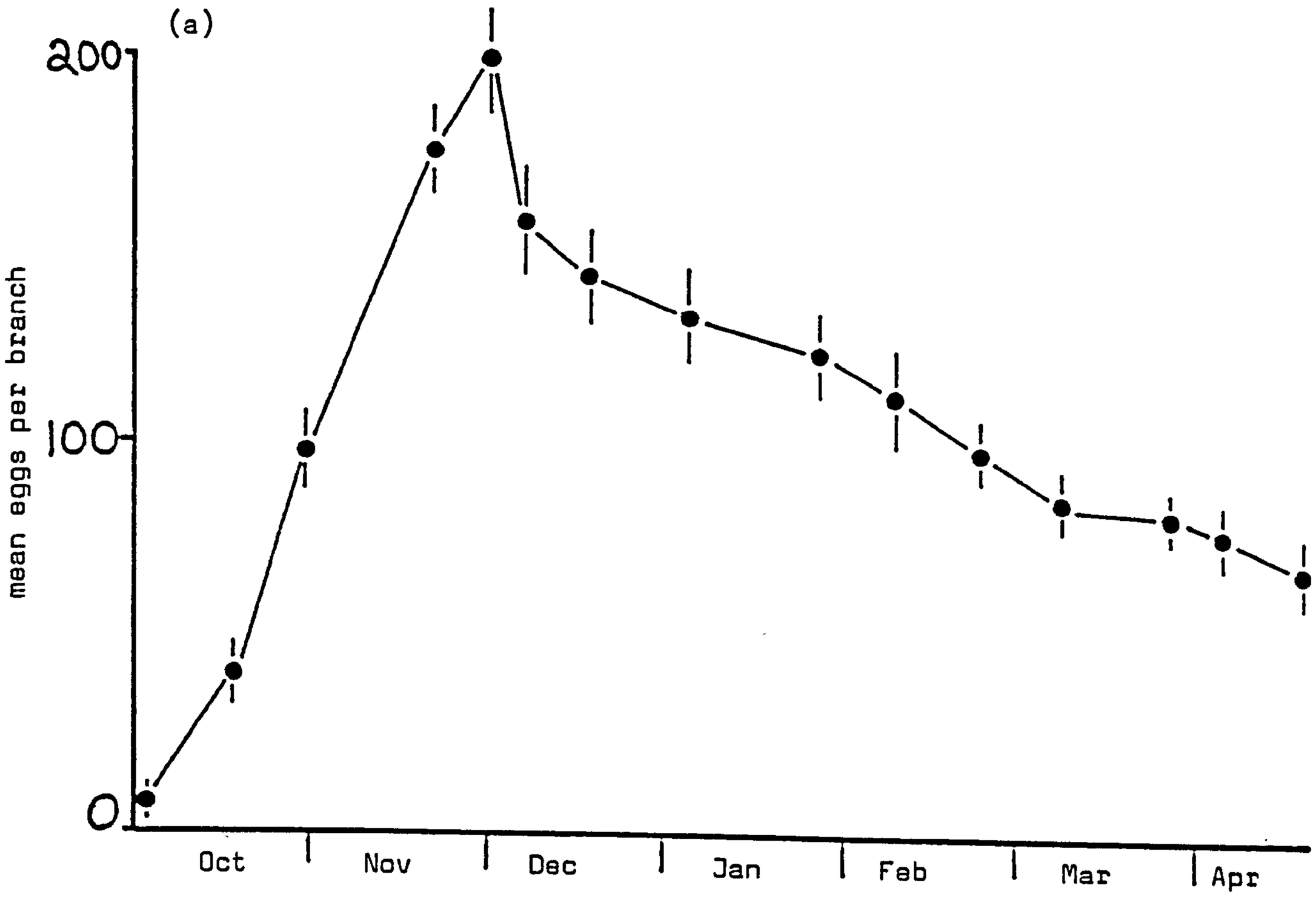


Figure 155: The proportion of P.alni eggs remaining with time on LF 125.



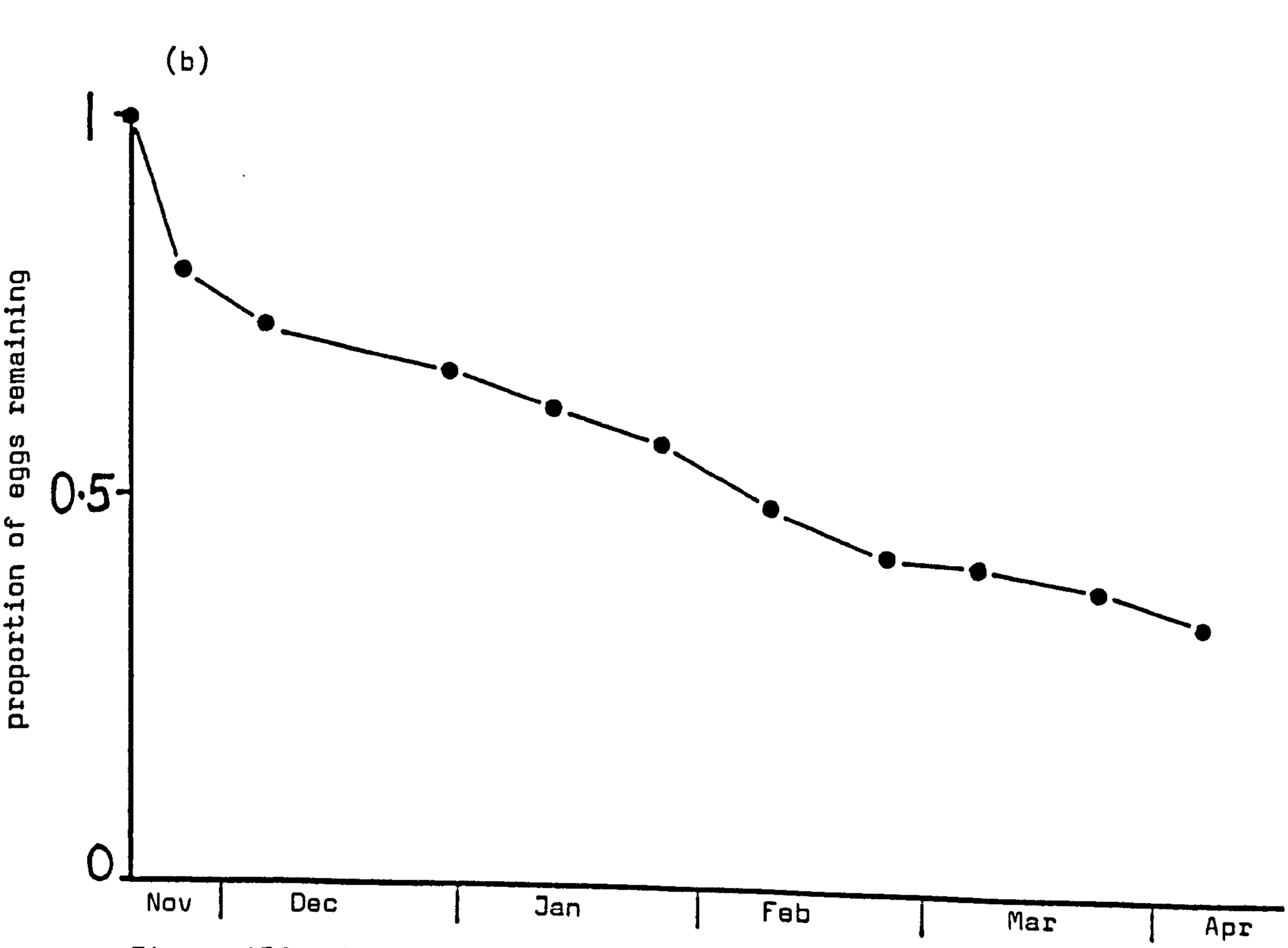


Figure 156: Abundance of P.alni eggs (whole branch samples), LF 125, 1983-84.

$y = -0.022x + 0.782$ ($r = -0.838$, d.f.=9, $p < 0.01$) in 1982-83 and

$y = -0.028x + 0.836$ ($r = -0.910$, d.f.=9, $p < 0.001$) in 1983-84. For the branches in 1983-84 this was $y = -0.026x + 0.836$ ($r = -0.947$, d.f.=9, $p < 0.001$). Thus the bud sampling method appears to be comparable to that of the intensive branch sampling.

The eggs which were present on the caged branches in mid April were counted and mortality expressed as a percentage of those present in the autumn. Eggs upon uncaged branches suffered a mortality of 65% (1429 eggs counted in autumn). Excluding birds reduced this figure to 58% (363 eggs counted) ($d=2.46$, $p < 0.05$). Eggs upon the branches caged in wire and netting suffered a mortality of 18.1% (409 eggs). This was highly significantly different from the uncaged branches ($d=16.94$, $p < 0.001$). Thus it appears that arthropods exert a considerable mortality on the eggs of P.alni. Although a variety of birds were noted upon the windbreak, notably Goldcrests, Regulus regulus anglorum Hart, Coal tits, Panus ater britannicus Sharpe and Dresser and Blue tits, Panis caeruleus obscurus Prazak, these did not appear to inflict a substantial mortality on egg numbers. It is likely that the birds are attracted to the seed-bearing cones rather than the aphid eggs.

If the bud samples are considered, these showed a 68% mortality of eggs from the peak in numbers to those recorded in mid April. There was no significant difference between this and the mortality of 65% reported upon the branches ($d = 1.86$, $p > 0.05$). This confirms the fact that bud sampling is a reliable estimator of egg mortality.

4.5. EGG HATCH AND BUD BURST

4.5.1. Introduction

Dixon (1976a) reported on the egg hatch of D.platanoidis and bud burst of sycamore. It was found that egg hatch and bud burst did not always coincide and varied from year to year. Differences were attributed to temperature variations between years.

In this section the pattern and timing of bud burst of A.glutinosa, A.cordata, A.incana at East Malling and at Lyne with the addition of A.hybrida is reported. Egg hatch of P.alni at each locality was recorded and is also presented.

4.5.2. Materials and methods

Bud burst and egg hatch was investigated at Lyne in 1982 and 1983 and at East Malling in 1983 and 1984.

At Lyne five branches were selected from trees of the four alder species present. Buds were examined twice weekly from the beginning of March and the number burst recorded. A 'burst' bud was defined as one in which the bud scales had parted sufficiently to expose leaf tissue which would afford a feeding site for an aphid. From mid April onwards aphids began to appear on the leaves. All nymphs that hatched were removed and counted on each sampling occasion. Branches were chosen which were not overhung to a great extent by others, thus minimizing the possibility of aphids falling on to them from above. The bases of the branches were ringed with Oecotak to prevent aphids walking on to the branch. These branches were not the ones used in the sampling programme.

The same procedure was used at East Malling. All branches chosen were on the opposite, unsampled faces of the windbreaks.

4.5.3. Results

At Lyne bud burst followed a very similar pattern in both years (fig.157a,b,). First to break its buds was A.hybrida which began in early March. In this species, bud burst was complete by late March. A.incana began bursting next, followed by A.glutinosa. In these species bud burst was complete by early May. A.cordata was the last to burst, beginning in mid April and finishing in mid May. Aphid hatch was very similar in the two years; beginning in mid April and ending by early May (fig.157c).

At East Malling bud burst was followed on LF125, WM110,WM109 and LF126 (A.incana and A.cordata). Aphids were numerous on LF125 and egg hatch was followed on this windbreak. The results are presented in figs.158 and 159.

Patterns of bud burst and aphid hatch showed some differences between the years. Bud bursting of A.glutinosa began earlier in 1983 but the proportion in 1984 rapidly caught up, such that all was complete by the end of April (fig.158). There appeared to be no differences between windbreaks which had been cut during the previous summer or winter. A incana also began bud bursting earlier in 1983 but subsequently followed a similar pattern to A.glutinosa. A.cordata was last to burst. It too began bursting earlier in 1983.

The pattern of egg hatch (fig.159a) was also different between the two years, being initially faster in 1983 then becoming slower. To determine whether the difference may have been due to temperature the percentage egg hatch was plotted against day degrees from the beginning of April (fig.159b). When the daily percentage hatch was compared between the two years, there was no

Figure 157:

Bud burst and aphid hatch at Lyne

(a) bud burst, 1982

(b) bud burst, 1983

..... A.hybrida

——— A.incana

– – – – A.glutinosa

—·—·—· A.cordata

(c) aphid hatch

——— 1982

– – – – 1983

(a)

100

50

0

Per cent of buds burst

(b)

100

50

0

Per cent of eggs hatched

(c)

100

50

0

March

April

May

Figure 158

Bud burst at East Malling

(a) LF 125, section 1

(b) LF 125, section 2

(c) WM 110, section 1

(d) WM 110, section 2

(e) WM 110, section 3

(f) LF 126, A.incana

(g) WM 109, section A

(h) WM 109, section B

(i) LF 126, A.cordata

——— 1983

– – – – 1984

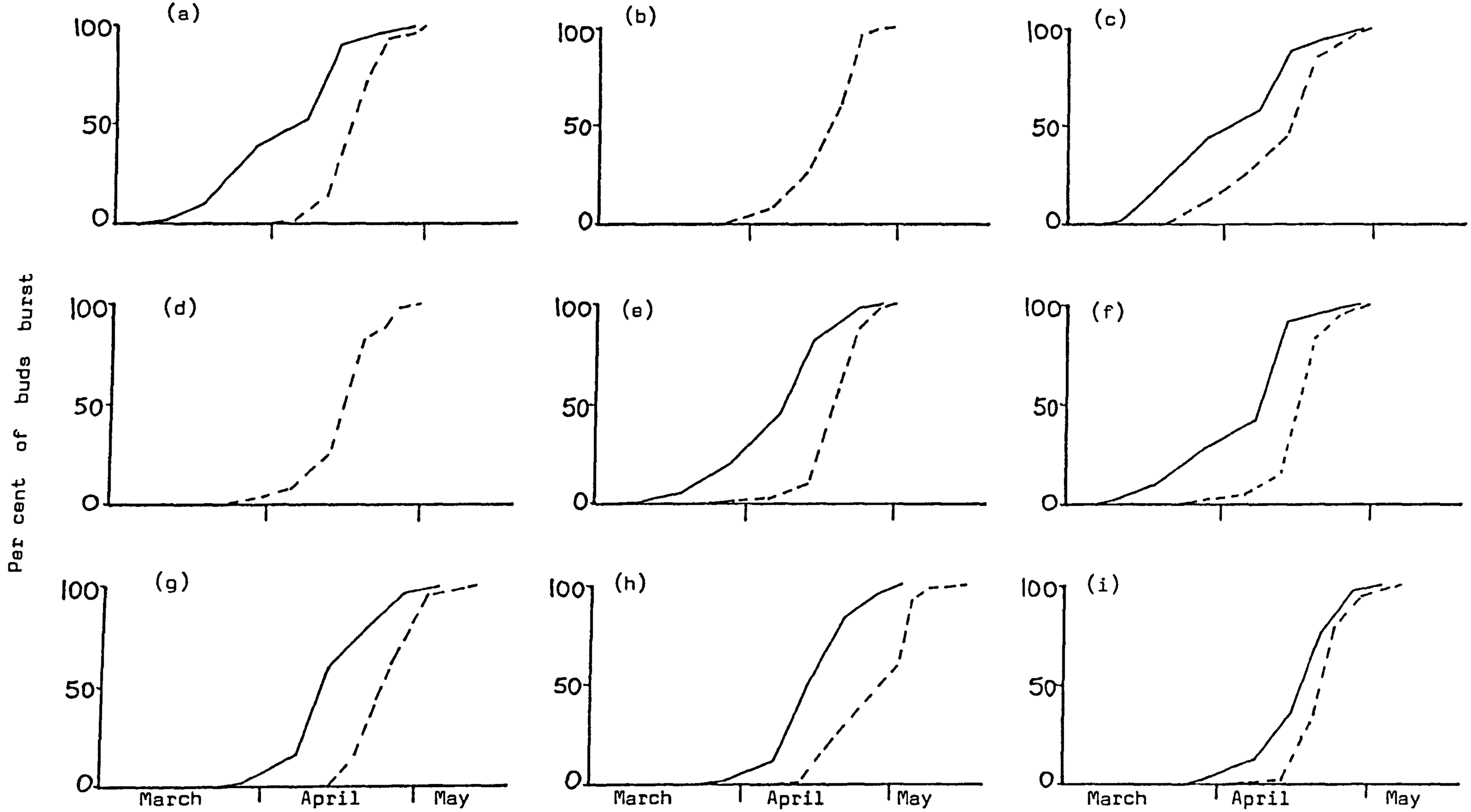

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
100
50
0
Per cent of buds burst
March
April
May

Figure 159:

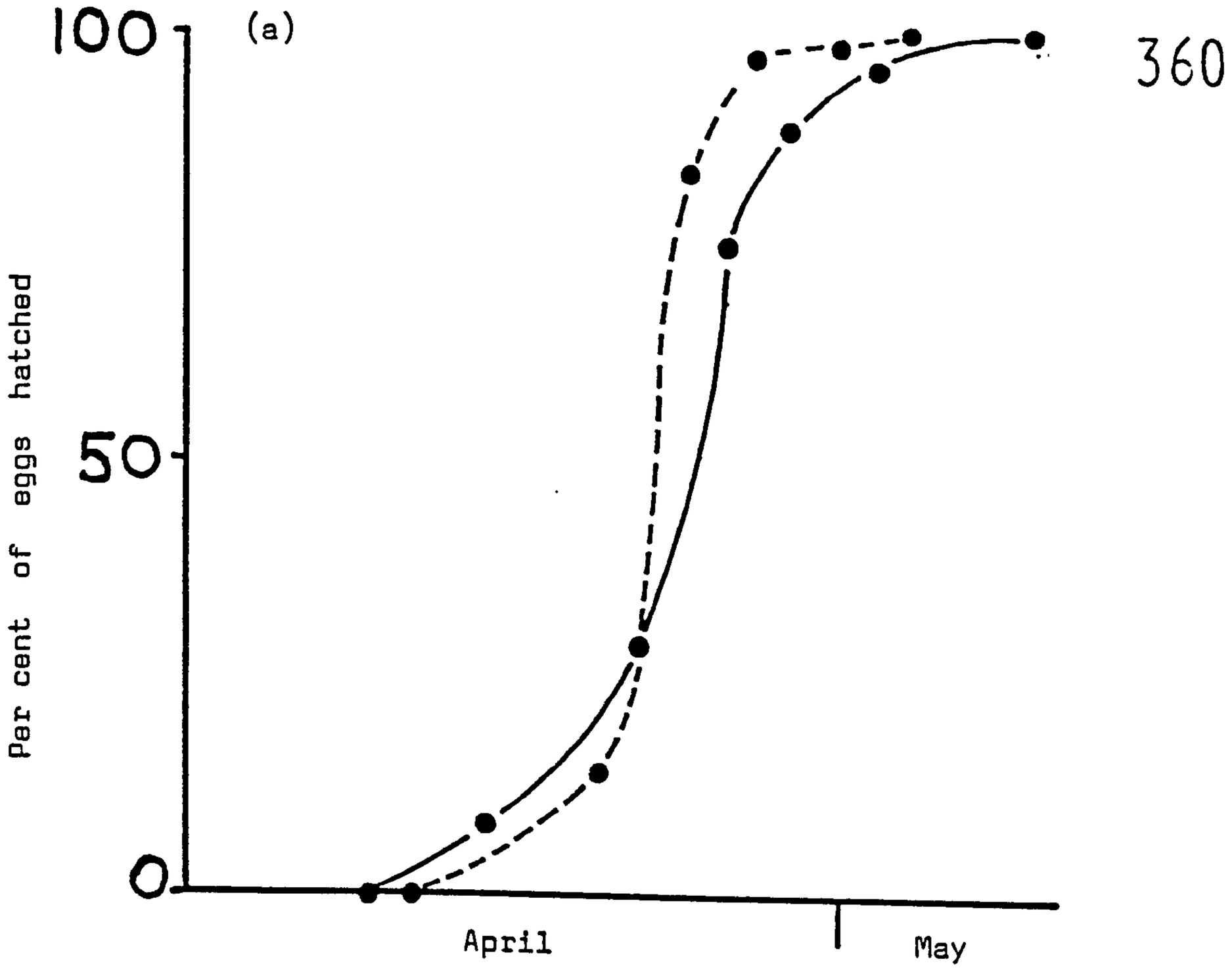
Egg hatch of P.alni at East Malling in

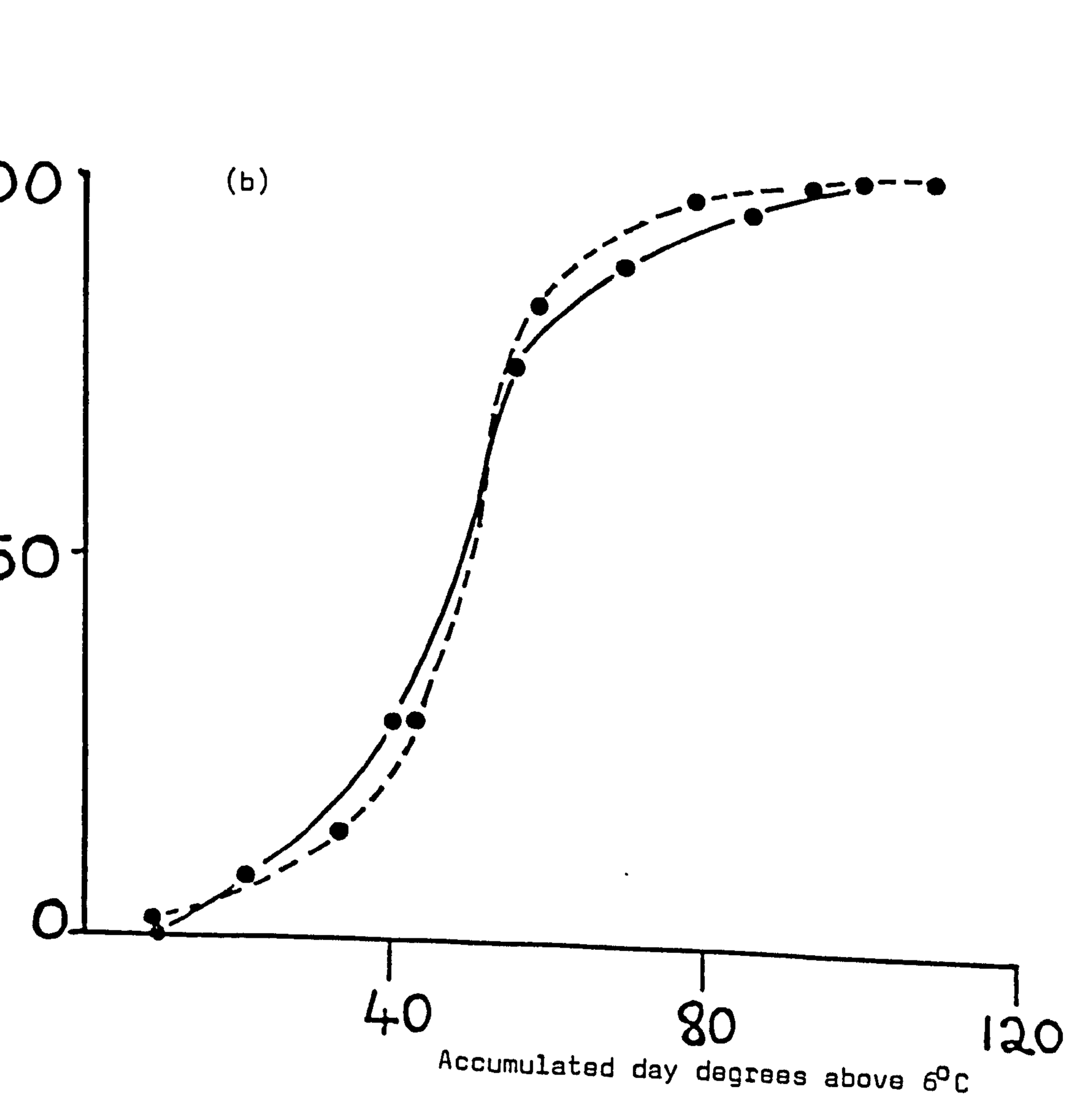
——— 1983, and

- - - - 1984

(a) relative to time

(b) relative to temperature


(a)
100
50
0
Per cent of eggs hatched
360
April
May


(b)
100
50
0
Per cent of eggs hatched
40
80
120
Accumulated day degrees above 6°C

significant difference in the average time of egg hatch. For 1983 this was 24.6 days and 1984, 23.0 days ($d= 1.25, d.f.=8, p>0.05$). However, there was a significant difference in the variance between the years ($F_{4,4} = 34.04, p<0.01$). When the average egg hatch was expressed in day degrees there was no difference in the time or in the variance. For time the mean was 61.7 day degrees (1983) and 59.0 day degrees (1984) ($t= 1.43, d.f.=8, p>0.05$). For variance, $F_{4.4} = 3.07, p>0.05$). This strongly suggests that the difference in egg hatch observed in the two years was due to temperature differences. The daily accumulated day degrees above $6^{o}C$ for April 1983 and 1984 are shown in fig.160. It can be seen that early April 1983 was warmer than 1984 with the converse holding for the latter part of the month.

From the preceding data it can be seen that at the time of egg hatch there are leaves available for the aphids to feed upon. The mortality at this time may therefore be less than an aphid such as D.platanoidis which hatches before bud burst and must remain upon them until this event occurs (Dixon, 1976a).

Five branches were selected from LF125 and the number of first generation aphids upon them counted at twice weekly intervals from mid-April until late May. Branches were selected so as to minimize aphids falling upon them from above and their bases ringed with Oecotak. The mean number of fundatrices recorded per branch is depicted in fig.161a. Numbers reached a peak in early May, thereafter showing a steady decline. The decline was more rapid in 1983 and a greater percentage of aphids disappeared (33.6% in 1983; 12.5% in 1984). The daily rainfall for the period is given in fig.161 b,c. More rain fell in May 1983 than 1984 and heavier falls appeared to be associated with aphid decline in that year. Although not conclusive proof, these observations imply that heavy rain has an effect upon early spring populations of aphids. This supports the observations

Figure 160:

Accumulated day degrees during April at

East Malling

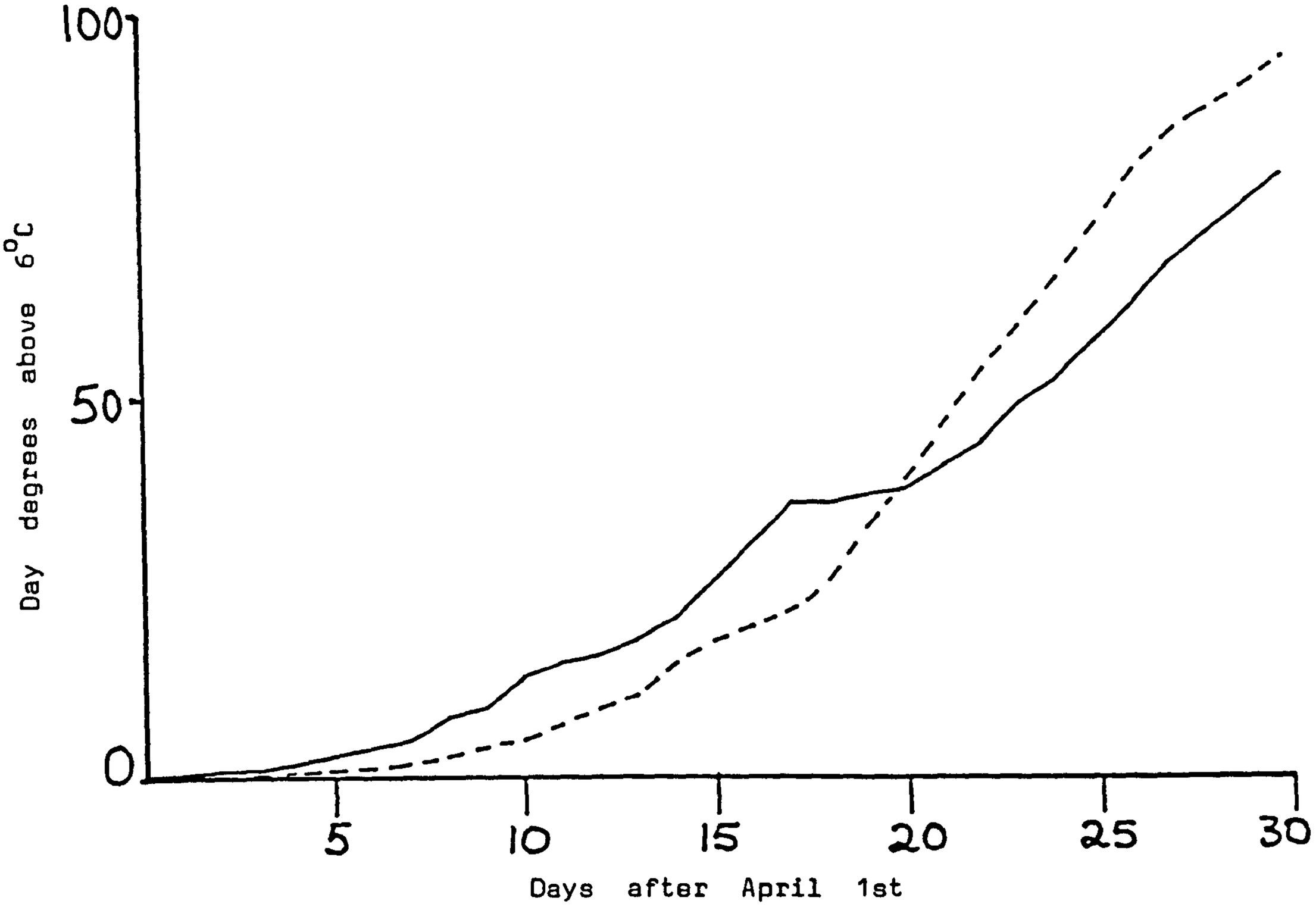
——— 1983

— — — — 1984

(a) Above $6^{o}C$

(b) Below $6^{o}C$

(a)


100
50
0
Day degrees above 6°C
5
10
15
20
25
30
Days after April 1st

(b)

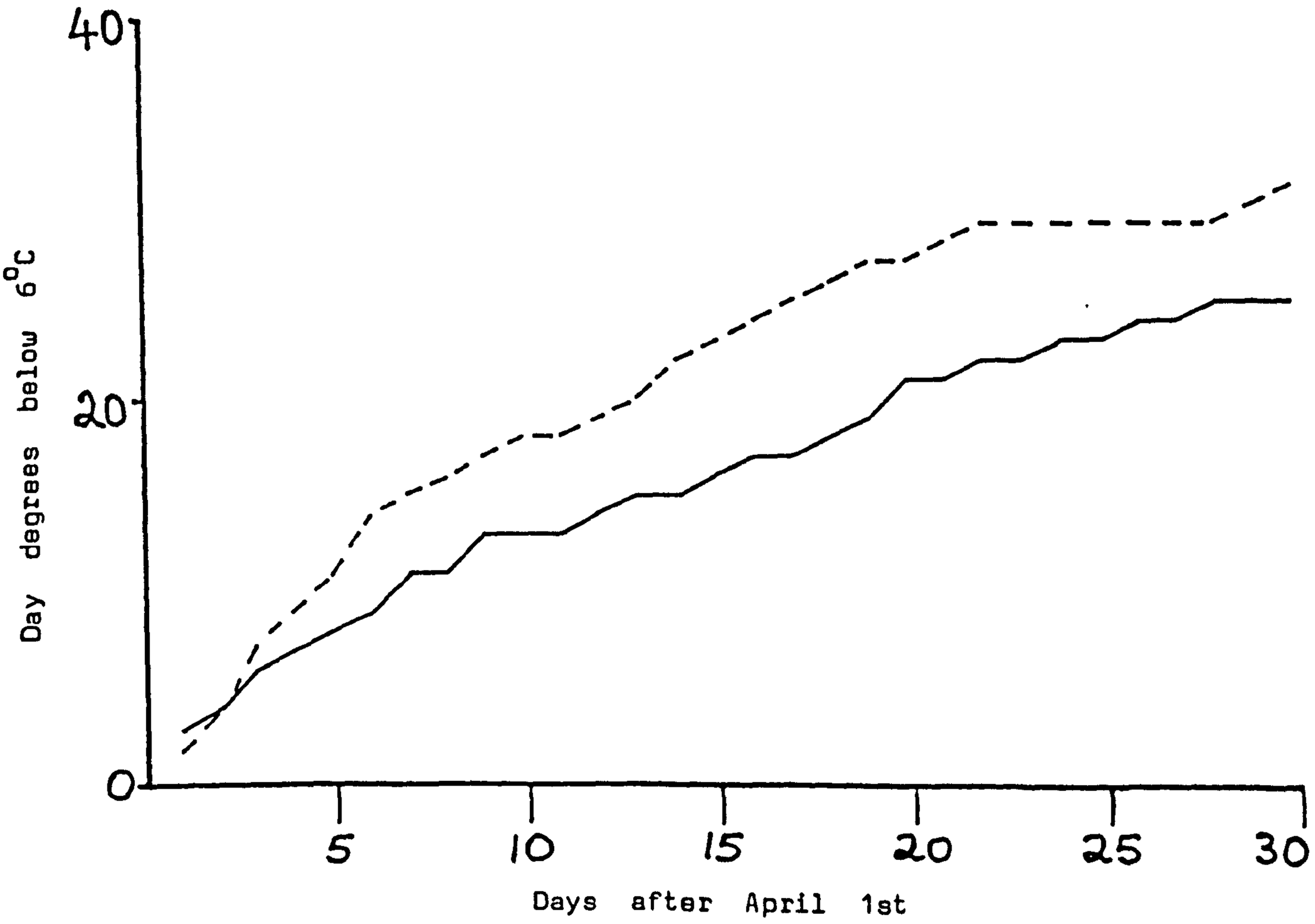

40
20
0
Day degrees below 6°C
5
10
15
20
25
30
Days after April 1st

Figure 161:

Abundance of first generation aphids and rainfall

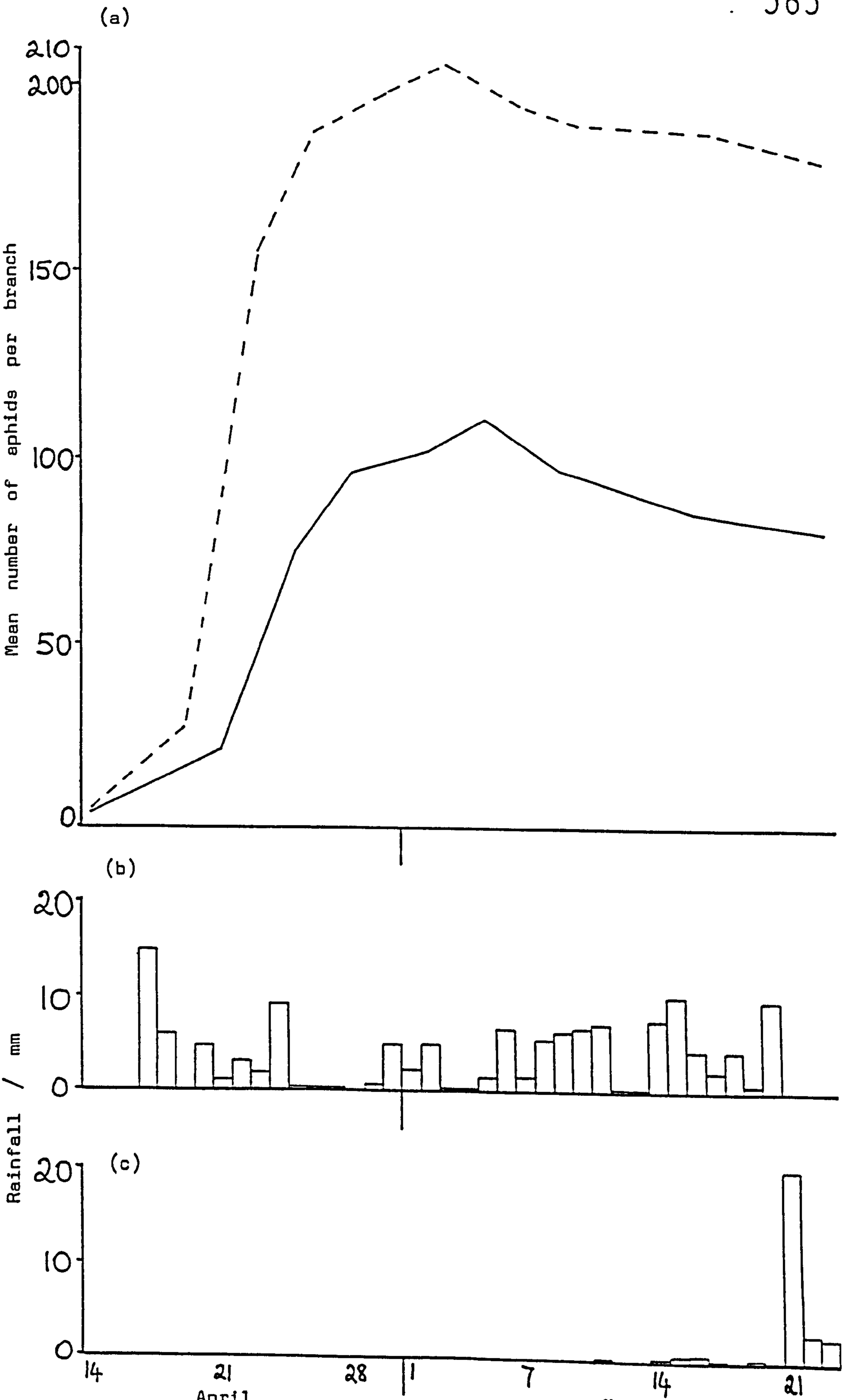
at East Malling

(a) Aphid numbers on branches

—— 1983 - - - 1984

(b) Rainfall, 1983

(c) Rainfall, 1984


(a)
210
200
150
100
50
0
Mean number of aphids per branch
(b)
20
10
0
Rainfall / mm
(c)
20
10
0
14
21
28
1
7
14
21
April
May

at Lyne in 1982 where heavy rain in May had marked effects on aphid numbers (chapter 2).

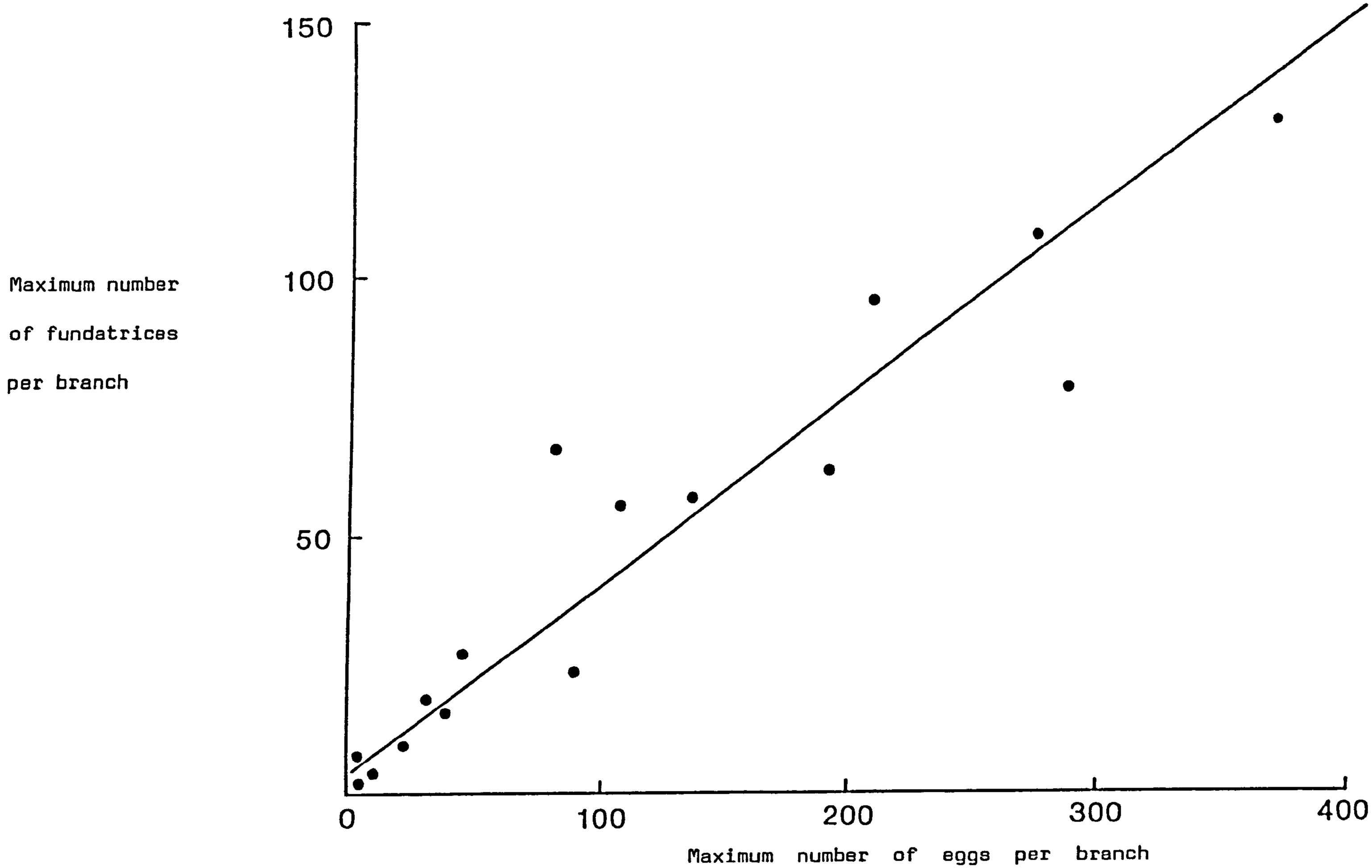
The peak number of fundatrices on sixteen branches from LF125 and WM110 (out of the 25 branches sampled on these windbreaks, 9 had no eggs upon them) in spring 1984 showed a good relationship with the maximum number of eggs laid upon them in November 1983 (fig.162: $r = 0.891$, d.f.=14, $p < 0.001$). Thus the more eggs which are laid in autumn, the higher the number of fundatrices present the following spring.

4.6. DISCUSSION

The apterous oviparae of P.alni are heavier at maturity than any other morph of this aphid (c.f.chapter 5). In comparison, the winged males are considerably smaller. A possible explanation for the size of the oviparae is that they appear to mature all the eggs together, soon after reaching adulthood, so that the abdomen becomes packed and distended. A similar occurrence was noted by Shands, Wave and Simpson (1961) with the foxglove aphid, Myzus solani (Kaltenbach). In that study however, the retention of eggs compared to the other species sampled (M.persicae and M.euphorbiae) could have been due to differences in the plant sampling techniques employed. These results indicate that P.alni matures all its eggs together and then lays them soon after mating. If an ovipara is unmated, eggs are not laid quickly but only after a period of about 3-4 weeks. The egg laying habits of A.fabae were recorded by Blackman (1974) who stated that all the eggs laid were produced within an hour or so of mating. P.alni does not lay as quickly as A.fabae and the laying process is affected by temperature. At $10^{o}C$, 58% of eggs are laid in the first seven days after mating, whereas at $15^{o}C$ this figure rises to 88%. During October 1983 and 1984 at East Malling, the average daily temperature fell from $15^{o}C$ during the first week to $12.5^{o}C$ during the second week, to $9.5^{o}C$

Figure 162:

Relationship between the number of eggs on a branch and the number of fundatrices on the branch subsequently.


150
100
50
Maximum number
of fundatrices
per branch
0
100
200
300
400
Maximum number of eggs per branch

during the third. It is therefore likely that oviparae in the field will deposit about 60% of their eggs during the first week after mating. Males are most abundant in early October and oviparae in late October. Males can overcome their numerical disparity by flying in search of oviparae and fertilizing more than one. It is likely that in late October egg laying is a fairly slow process due to the temperature. This probably accounts for the peak in egg number, as measured by bud samples, occurring in mid-late November.

The weight and egg content of oviparae when reared on regrowth foliage is considerably reduced. This leaf tissue provides a very poor food supply for the aphids (chapter 5). Windbreaks are generally pruned between mid July and mid August. The later in the season when this event occurs, the less the extent of the regrowth. It is unlikely that pruning would seriously affect ovipara weight and fecundity in the field as regrowth was never very extensive and no oviparae were ever found upon such leaves in the leaf samples.

The number of eggs laid by P.alni under constant conditions is about 15; therefore the full egg complement is realized. Under natural conditions this number is considerably reduced to about 6. The reduction may reflect some of the mortality factors acting upon the oviparae. Such factors are likely to include weather, notably wind and rain, insect and bird predators. Autumns with little wind allow the sycamore aphid to attain high levels of abundance (Dixon,1977). The effect of wind upon this aphid was quantified by Chambers (1979). Insect predators such as anthocorids and coccinellids both of which hibernate as adults were recorded upon the windbreaks throughout the autumn, thus it is likely that a substantial number of oviparae fall prey to these insects. Oviparae are a readily acceptable food source for anthocorids. One adult female A.nemorum which had been starved for four days was placed in a tube with a number of unmated

oviparae. The bug immediately began feeding, consuming six aphids before being apparently satiated.

All oviparae released in the field were assumed to be mated. Under natural conditions it is likely that not all oviparae would be fertilized, thus reducing the average number of eggs laid still further. Egg production by oviparae has been recorded by other authors for a range of aphids. In extreme cases, members of the Eriosomatinae lay one egg (Hille Ris Lambers, 1966). B.asparagi (Tamaki et al,1983) produced an average of 10.5 eggs in caged conditions. P.humuli produced 4-7 under laboratory conditions (Tsvetkov, 1962) and A.fabae 4-6 (Blackman, 1974). Brown (1975) working with E.tiliae found that the mean number of eggs laid was related to the size of the ovipara and that this depended on the population density. Small oviparae produced about 1 egg each; larger ones producing about 5. Searle and Mittler (1982) found that egg production in M.persicae was affected by photoperiod. The egg laying patterns of oviparae were affected by the rearing conditions of the gynoparae and oviparae. Long night conditions during development of gynoparae and oviparae resulted in 'normal oviparae'which did not oviposit in the first two to three weeks of life unless mated. Keeping gynoparae and oviparae in short night conditions resulted in oviparae which resembled apterous virginoparae but which began to lay unfertilized eggs 2-3 days after becoming adult. P.alni thus resembles M.persicae in that unfertilized oviparae do not lay immediately. The low number of eggs in oviparae of P.alni (never more than 3 in any ovariole) compared to embryos in an apterous virginoparae (c.f.chapter 5) ensures an abundant supply of nutrients for these eggs and enables the oviparae to deposit most of their eggs soon after mating. This would be advantageous in natural conditions when mortality factors in autumn are many and varied. More eggs would therefore be produced if feeding could be prolonged.

Oviposition sites favoured by P.alni are the axils of buds on first year growth and crevices in older bark. Over half of the eggs laid are upon the first year growth. The proportion laid upon this growth remains relatively constant, regardless of the total numbers of eggs or the removal of the growth by summer pruning. Sampling first year twigs, therefore, means that a constant proportion of the eggs present are sampled; a similar finding to that of Cammell et al (1978) with A.fabae on spindle. Sampling the buds of that first year growth also represented a constant proportion of eggs present. The relationship was found for pruned and unpruned branches, indicating that sampling the first year buds could provide a reliable estimate of the total eggs present, similar to the study of A.fabae (Cammell,et al, 1978).

Most eggs were laid in the middle area of the branches, this being associated with the increased amount of available oviposition sites, caused by more side branches in the middle. This is in contrast to D.platanoidis eggs on sycamore (Dixon,1976 a) where most eggs were found more than 50 cm. from the terminal bud and the egg density increased with distance.

Pruning branches in winter removed on average 25% of the eggs present and 41% of the buds. Most of the wood removed was the previous year's growth and therefore the majority of eggs lost were on the first year wood.

The natural mortality of P.alni eggs was found to be linearly related to time from the point when the maximum egg number occurred. Eggs died at a rate of about 3% per week. A similar relationship was reported for R.padi in Finland (Leather and Lehti,1981), in which the mortality was estimated to be 5% per week. The difference in mortality rates is unlikely to be a result of the severity of Finnish winters (Leather,1981) and may be a result of predation. A.nemorum which is active on the windbreak hibernates as an adult when the weather becomes more severe. According to Hill (1957)

hibernating adults are not active in December, January and February in Scotland. In Southern England, however, the bug may not hibernate until January, feeding on the aphid eggs previously, as described by Hill. This may account for the marked drop in egg numbers in early winter and the levelling out of egg loss as winter progresses. Way and Banks (1964) also noted A.nemorum feeding upon eggs of A.fabae during Autumn.

The overall egg loss in P.alni was found to be 65%. This is comparable to that reported for other aphid species and reviewed by Leather (1983). This mortality is mainly attributable to the action of arthropod predators, the mortality falling to 18% when these were excluded. Birds exerted a loss upon the eggs but this was considerably less than that imposed by insects. Leather (1981) considered that arthropod predation was the main cause of mortality in eggs of R.padi and Way and Banks (1964) reporting on the high survival rate of A.fabae eggs recorded that some eggs were lost to anthocorids and birds. In the present study mites were not excluded by the netting cages used. Way and Banks used voile-covered cages which excluded mites. It is possible that predatory mites such as Typhlodromus pyri Scheuten which overwinter as adult females in bark crevices (Alford,1984) were not excluded and exerted some influence upon the mortality of the eggs.

Temperature was not recorded within the netting covered cages and it is possible that differences existed inside and outside the cage. Humidity may also have varied due to the netting and it is possible that changes in these factors may have affected egg survival. Rain was obviously reduced in the netting cages and any effect it may have had on eggs would thus have been unapparent. Dunn and Wright (1955) considered that rain promoted fungal infection and dislodged eggs of A.pisum. Leather (1981) stated that rain had little or no effect on eggs of R.padi in East Anglia.

Using estimates of egg loss due to pruning and that from natural causes, it

is possible to estimate when pruning would have least or most effect upon aphid numbers. Using an 'ideal' relationship of y=1-0.022x, developed from the proportion of eggs surviving with time (fig.155) it is possible to predict the number of eggs surviving. If a population consisted of 1000 eggs, after 20 weeks this would have been reduced to 560. If this population was pruned at the egg peak, resulting in 25% loss, the number remaining after 20 weeks would be 420. If the population was pruned after 10 weeks the number remaining would be 456. Thus if one requires to preserve eggs, the windbreak should be pruned in mid winter, after the initial drop in egg mortality has occurred. Higher numbers of eggs which overwinter result in higher numbers of fundatrices in spring (Way and Banks, 1968, Dixon,1976a). It has been shown that for P.alni higher initial numbers result in earlier aphid population peaks (chapter 2). The effect of this on bug migration from the windbreak is discussed in chapter 6.

Sampling of buds provided a quick and reliable method of monotoring egg abundance. It appeared to be directly comparable to the more intensive method of branch examination and was sensitive enough to detect small changes in numbers over short periods of time. Therefore, as found by Leather and Lehti (1981) bud sampling fulfills all the criteria of a successful sampling method (Southwood,1978).

Unlike D.platanoidis on sycamore (Dixon 1976a) egg hatch of P.alni is closely synchronized with bud burst of its host, A.glutinosa. It is interesting to note that the different alder species exhibited very different patterns of bud burst. A.incana bursts early in the year. This tree is introduced to Britain and is a native of northern Europe. It therefore experiences a colder climate in its native habitat and burst early in the relatively warmer British spring. The opposite applies to A.cordata, a native of the Mediterranean region. This bursts relatively late, when the climate is warmer in May. A.hybrida burst very early in the year and this may be a result of 'hybrid vigour' with the early bursting character

inherited from A.incana. P.alni is therefore synchronized with its native host plant A.glutinosa. Eggs begin to hatch when about half of the alder buds have burst, thus fundatrices will have leaf material to feed upon immediately and the leaves will be very young. These leaves provide a rich food source for the aphids. Aphids which are reared on mature leaves may be considerably smaller than those on young leaves (Dixon,1970b). It is therefore an advantage for fundatrices after hatching to move on to very young leaf tissue. Such a situation would be less likely to occur if a fundatrix hatched on A.incana or A.cordata. Even if the food supply was the same, leaves of A.incana would be older at egg hatch than those of A.glutinosa whereas those of A.cordata would not have unfurled. The synchronization of bud burst and egg hatch is important for P.alni. Because the fundatrix is apterous, flight of early maturing adults cannot occur in spring, unlike D.platanoidis (Dixon,1974). The winged first generation aphids of D.platanoidis can move between trees, thus enjoying maximum exploitation of the habitat. Late bursting sycamore trees which did not afford a food supply to the first generation nymphs may thereby provide a rich food source for the adults of the first generation and their offspring. It was noticeable that the late bursting of A.cordata did not appear to afford a satisfactory food supply and the aphids which hatched upon it (WM109,1983) did not initiate a population.

The differences in egg hatch and bud burst between years was largely attributable to changes in temperature. Chambers (1979) found that sycamore trees tend to burst their buds later in a year following high aphid numbers the previous autumn and quantified this relationship. However, it was also found that egg hatch might be delayed after years of high density enabling the aphid to 'catch up' with the postponed bud burst of its host. Despite the lack of information available for alder it appears that this may not occur. The population density of oviparae on LF125 in autumn 1982 was 2.7 times that in 1983, yet bud burst was earlier in 1983 than 1984.

Egg hatch was also earlier in 1983. The fact that uninfested trees of A.incana and A.cordata and other windbreaks of A.glutinosa also burst earlier in 1983 suggests that temperature was the causative factor.

Because it hatches before bud burst, mortality of fundatrices of D.platanoidis is high (Dixon 1976). This was mainly attributed to the action of rain and birds. This is a high price to pay to ensure that the aphids feed on the youngest leaves. However the advantages are great. Aphids which hatched early on bursting trees matured in time to colonize other trees whose leaves were just unfurling, thus exploiting the rich food source to the full. An extreme example of this was provided by Periphyllus testudinaceus (Fernie) (Shearer, quoted in Chambers,1979) on European maple. In this species fundatrices hatch in early February and are adult just before bud break, resulting in high fecundity and rapid growth rate of the second generation nymphs. The mortality must be very high during the pre-bud break period. Differences in bud burst between trees in a year was noted for A.glutinosa and appeared to be more marked in A.incana. However, in no case did aphids hatch on a branch before a proportion of the buds had burst. Generally this proportion was about 50% and at least 26%. Thus fundatrices hatching on A.glutinosa can readily find a highly favourable food source. The greatest part of aphid hatch occurs as the last buds break. Mortality still occurs at this time possibly due to the action of wind and rain, but is also a likely result of predation by anthocorids and coccinellids emerging from hibernation.

There was a good relationship between the peak number of eggs on a branch and the maximum number of fundatrices recorded upon the branch. High numbers of eggs laid in autumn thus result in higher numbers of fundatrices the following spring.

Chapter 5. FOOD QUALITY, GROWTH AND REPRODUCTION OF P.ALNI

5.1. THE SOLUBLE NITROGEN AND WATER CONTENT OF ALDER LEAVES

5.1.1. Introduction

Aphids feed almost continuously throughout nymphal and adult life (Blackman, 1974). Most aphids feed by inserting their stylets into the phloem elements of plants. In a healthy plant the phloem sap is under pressure and thus readily flows up the aphid's food canal and into the pharynx. Kennedy and Mittler (1953) were able to obtain phloem sap by severing stylets of Tuberolachnus salignus (Gmelin) feeding on willow twigs and collecting the exudate. Although a wide range of sugars have been recorded in phloem sap, the only one present in any quantity is sucrose, generally accounting for 10-25% (Blackman, 1974). Amino acids and amides are found in concentrations of between 0.2 and 0.5%, rising to about 5% during senescence and bud burst (Llewellyn, 1984). These compounds are the major nutrients which aphids utilize for growth and body maintenance. The study of the requirements of different amino acids by aphids has been aided by work involving aphids feeding on artificial diets through 'parafilm' membranes. An example is the work of Dadd and Krieger (1968) who reported that methionine, histidine and isoleucine were required by M.persicae. Although the sap of a plant may be poor in nitrogenous compounds, aphids imbibe sap so fast that they may take in more nitrogen than can be used. Mittler (1958) found that most of the amino-acids and amides in phloem sap were present in smaller quantities in the honeydew excreted. The ingestion of large quantities of sap can represent a considerable drain on the resources of the host plant. Llewellyn (1972) reported a consumption of 3672 Kcal/m^2/year for E.tiliae on lime and Van Hook, Nielsen and Shugart (1980) recorded that Illinoia (Macrosiphum) liriodendri (Monell) consumes 400% of its dry body mass per day and that an aphid population on Liriodendron tulipifera L. consumed 1% of the annual photosynthate production and 17% of the annual standing crop of foliar nitrogen.

The percentage of soluble nitrogen in leaves is a good indicator of the nutritive quality of this tissue for aphids (Dixon,1971d). The quality of food available to aphids has been shown to vary markedly during a growing season. Levels of amino-nitrogen are higher when leaves are actively growing and senescing as nutrients are carried into and out of the leaves at these times. Therefore, trees characteristically exhibit high levels of amino nitrogen in early spring and again in autumn. When the leaves are mature in summer the soluble nitrogen level is low and consequently the aphid's food source is poorer. Such patterns of amino-nitrogen levels have been reported for sycamore, Acer pseudoplatanus L. (Dixon 1963), lime, Tilia x vulgaris Hayne (Dixon 1971c), bird cherry, Prunus padus L. (Dixon,1971d), oak, Quercus robur L. (Lorriman,1980), sugar maple, Acer saccharum Marsh and yellow birch, Betula alleghaniensis Britton (Schultz, Nothnagle and Baldwin, 1980) and Hawthorn, Crataegus monogyna Jacquin (Sutton, 1984). When levels of soluble nitrogen are high, aphids tend to be large and highly fecund (Dixon,1963, 1970b,1971, 1971d). The low level of amino-nitrogen in the phloem sap of sycamore can be compensated for by D.platanoidis feeding at a higher rate (Dixon,1963). In field conditions this can only be achieved when the population is very low. When the population density is high this aphid ceases reproduction and goes into aestivation (Dixon,1966). The duration of aestivation is affected by crowding (Chambers, 1982). The aestivation period is longer when the aphids or their mothers are reared in crowds. D.platanoidis has an effect upon the nitrogen metabolism of sycamore leaves (Dixon 1971a). In years when aphids are abundant in spring, the leaves fall still rich in nitrogen in autumn. In autumns when large quantities of nitrogen are recovered from the leaves the aphids are large, have a high reproductive rate and reach high levels of abundance (1970b). This results in high levels of fundatrices the following spring leading to oscillating populations from year to year (Dixon, 1977). Other aphids have been shown to induce changes in their host plant quality. E.tiliae infestations on lime cause leaves

to be shed earlier in autumn and contain more nitrogen (Dixon, 1971b). Sluss (1967) considered that previously infested walnut leaves were a poor food source to C.juglandicola and Parry (1974) reported that low levels of essential amino acids resulted in population collapse of E.abietinum.

The chemical composition of A.glutinosa foliage was investigated by Wittwer and Immel (1981). It was found that alder foliage contained significantly higher levels of nitrogen than American sycamore (Platanus occidentalis, L.), river birch (Betula nigra L), green ash (Fraxinus pennsylvanica Marsh or a hybrid poplar (Populus sp.). This was attributed to the fact that alder is a nitrogen fixing plant (Bond,1967). In contrast to all the previously reported studies of the decline in soluble nitrogen in leaves, A.glutinosa appears not to follow such a trend, indeed quite the reverse (Dawson and Funk,1981). In a study in southern Illinois it was found that nitrogen concentration was low in spring, increased and remained stable throughout the summer with little decrease in autumn. Another study by Dawson, Funk, Fitton and Gertner (1980) indicated that a similar pattern occurred in A.serrulata (Aiton) Willdenow in the same locality. However, in this work, variation in A.glutinosa between localities was recorded. These authors also investigated the effect of leaf size on the nitrogen content. For one species, A.rugosa (Du Roi) Sprengel it was found that leaves with mid veins greater than 6cm in length followed the characteristic 'tree pattern' whereas leaves less than 6cm did not.

The soluble nitrogen fraction has been analysed (Virtanen and Miettinen, 1953) and compared with the pea plant. It was found that citrulline was the commonest free amino acid in alder, and commented upon that this had only been found in one other higher plant, the water melon.

There is therefore some suggestion that alder may show different patterns of soluble nitrogen abundance to that reported for other British trees. The availability of food to the alder aphid may thus be very different to

that for other species such as the lime or sycamore aphids. The soluble nitrogen content of A.glutinosa, A.cordata, A.incana and A.hybrida was examined throughout the aphid season from April to November during 1982 and 1983 at Lyne and 1983 at East Malling. The water content of leaf samples taken was also recorded.

5.1.2. Materials and methods

Random samples of leaves were taken at fortnightly intervals from bud burst in mid April to leaf fall in late November. Trees at Lyne whose branches were not sampled for aphids were used. At East Malling the opposite (non-sampled) face of the windbreak was used. Leaves were transported to the laboratory in an ice box and stored at $-20^{o}C$.

Leaf water was estimated by thawing a portion, removing surface water with absorbent paper, weighing and freeze-drying to constant weight. Soluble nitrogen was estimated using the method of Maltais and Auclair (1957) with the following modifications. Freeze dried leaves were ground to a fine powder in a ball mill and passed through a 500µm mesh sieve. 0.35g dry sample was transferred to a glass boiling tube and mixed with $15cm^{3}$ of acidified water at room temperature for 15 minutes. Samples were heated in a water bath at $100^{o}C$ for five minutes and centrifuged at 2,500 rpm for 10 minutes. The clear supernatant was removed, filtered through a $20cm^{3}$ Buchner funnel to remove any trace of the original sample and transferred to a $100cm^{3}$ Kjeldahl flask. Samples were digested with $10cm^{3}$ concentrated H_2SO_4 , $5cm^{3}$ H_2O_2 and 1 'Kjeltab' catalyst tablet (Thompson and Capper Ltd.). The digest was heated in 'Teccator' digestion blocks until it became pale green (1-1½ hours) and then refluxed for a further 30 minutes to ensure all the ammonia had been converted to ammonium sulphate (Allen,1974). The samples were left in racks to cool until just warm and then diluted to 50 cm^{3} with distilled water. Nitrogen

present was determined by Markham distillation where 5cm^3 portions of each digest were distilled with 5cm^3 40% NaOH and the distillate collected in 10cm^3 of Conway indicator (80mg Bromocresol green plus 160 mg Methyl red in 300 mls absolute ethanol. 15cm^3 of this mixture was added to 1 l of 2% Boric acid to make indicator solution). Distillation continued until the indicator turned from pink to green (with addition of ammonia from distillation) and then for a further 1½ minutes. The sample was titrated against N/70 HCl until the pink colour returned. Each sample was replicated three times and three samples were distilled from each digest.

5.1.3. Results

The seasonal change in water content of A.glutinosa, A.incana and A.hybrida leaves at Lyne is depicted in fig.163, and the soluble nitrogen content of these leaves in fig.164. In 1982 leaf water content was high when the leaves were very young in April at 70% of fresh weight. This figure fell throughout May to reach a level of 60% in early June. Thereafter the content varied little during summer with small rises in late autumn. A.incana exhibited the greatest drop in leaf water.

The soluble nitrogen content of expanding young leaves was 0.6% of dry weight and declined to 0.3% in late June. Analysis of variance of the arc-sine transformed percentages indicated no variation between the species but a significant difference in time (table 62).

The level of nitrogen rose quite sharply during July and August, reaching levels in early October which were similar to those in early May.

The patterns in 1983 were very similar to those of 1982. Leaf water content followed an almost identical decline to that of the previous year with the small rise in late autumn more apparent. There were no differences

Figure 163:

Seasonal trend in water content of alder leaves

at Lyne.

(a) A.glutinosa

(b) A.hybrida

(c) A.incana

●—● 1982

○—○ 1983

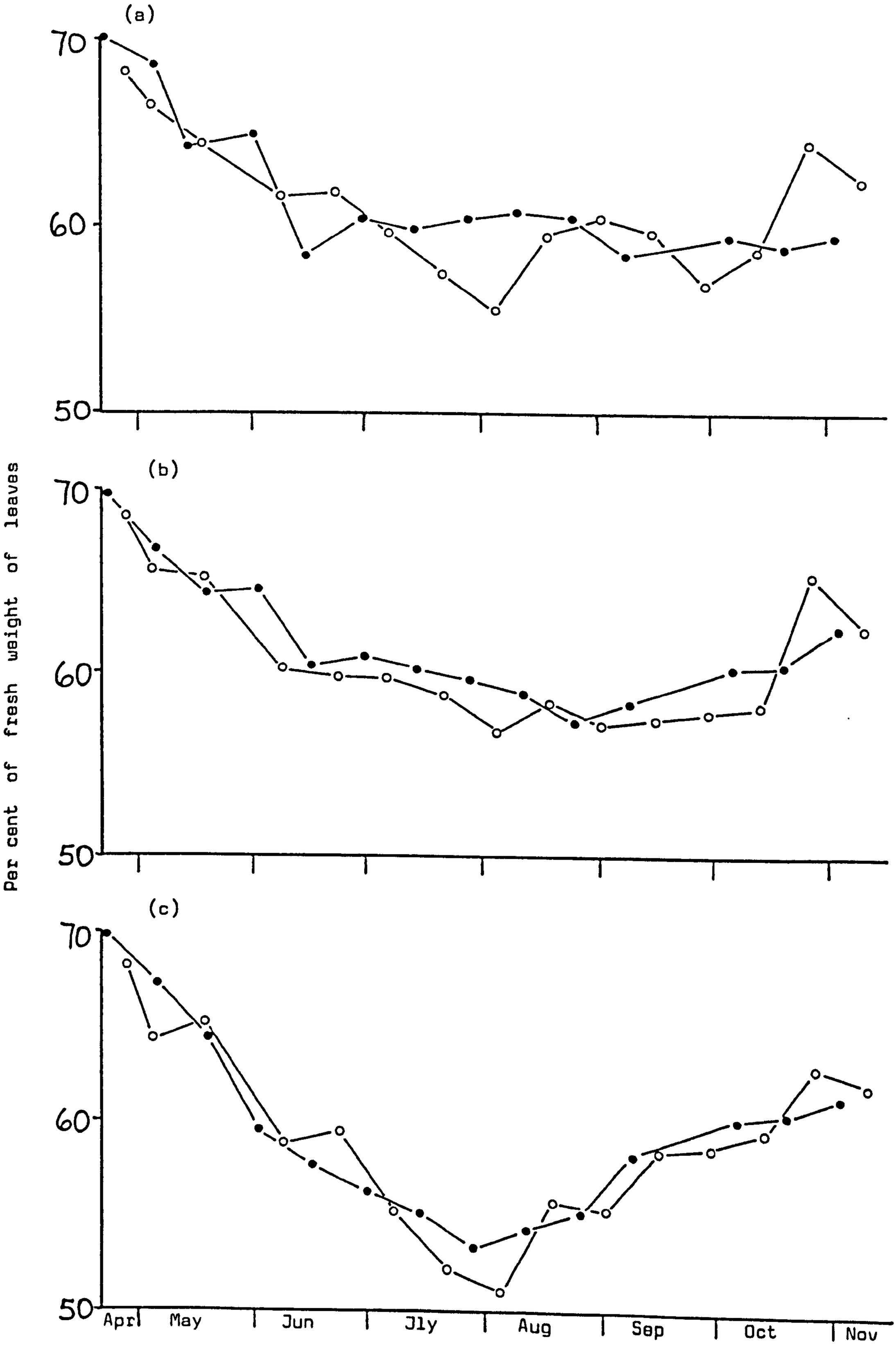

(a)
70
60
50
(b)
70
60
50
Per cent of fresh weight of leaves
(c)
70
60
50
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 164:

Seasonal trend in foliar soluble nitrogen at Lyne

(a) A.glutinosa

(b) A.hybrida

(c) A.incana

●—● 1982

○—○ 1983

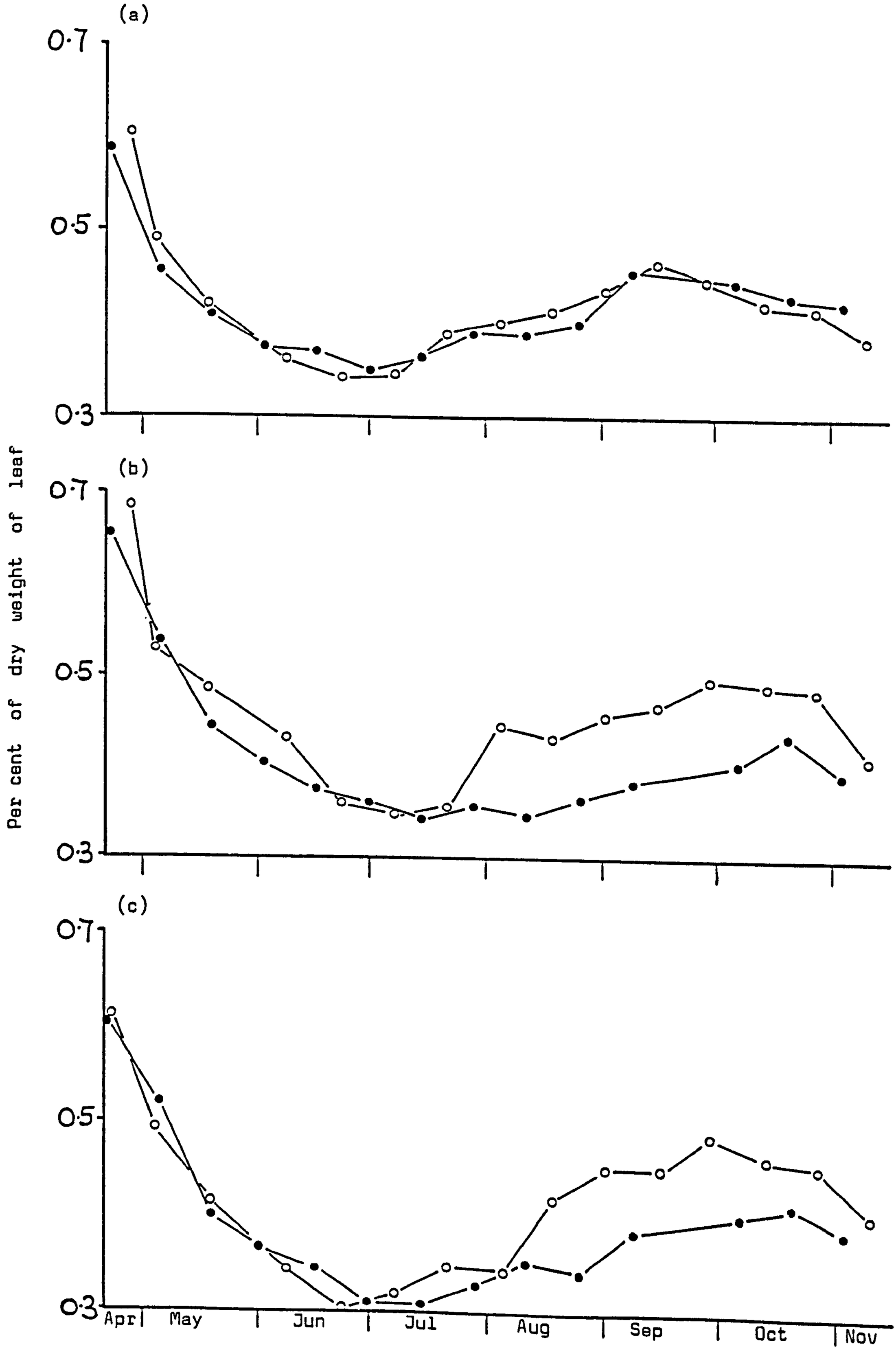

(a)
0·7
0·5
0·3
(b)
0·7
0·5
0·3
Per cent of dry weight of leaf
(c)
0·7
0·5
0·3
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Table 62: Anova for nitrogen contents of A.glutinosa, A.hybrida and A.incana; Lyne,1982 (Arc sine values computed)

Source of variation	Degrees of freedom	Sum of squares	F value	P
sample time	13	5.4006	17.227	<0.001
species	2	0.0142	0.294	>0.1
error	26	0.6269		
Total	41	6.0417		

Table 63: Anova for nitrogen contents of A.glutinosa (LF125) and A.cordata (LF126),1983 (Arc sine values computed)

Source of variation	Degrees of freedom	Sum of squares	F value	p
sample time	17	3.5560	6.19	<0.001
species	1	0.4429	13.11	<0.001
error	17	0.5741		
Total	35	4.5730		

between the nitrogen content of the three species in 1983 ($F_{2,26}$ = 0.426, $p > 0.05$) but again there were significant changes in time ($F_{13,26}$= 15.491, $p < 0.001$). The levels declined from 0.6% in late April to 0.3% in late June, rising to 0.47% in early October.

The results for the leaf water content of LF125, WM110 (A.glutinosa) LF126, WM109 (A.cordata) and LF126 (A.incana) at East Malling are given in fig.165, and the nitrogen levels for these windbreaks in fig.166. The patterns obtained were very similar to those at Lyne, with the content of A.incana falling most (fig.165f). There was no difference in soluble nitrogen between A.glutinosa and A.incana (LF125 v.LF126, $F_{1,17}$ = 0.581, $p > 0.05$), however there was between A.glutinosa and A.cordata (table 63). Although the levels of nitrogen were of the same order, the pattern of abundance through the season was different. Whereas A.glutinosa and A.incana nitrogen levels fell to a minimum in late June, the lowest point for A.cordata was reached in early August, after a shallower decline.

The differences were consistent between the windbreaks. On WM109 the low point was also reached on August 1st and on WM110 the point was reached in late June. There appeared to be no difference between the sections of WM110 (1V2, $F_{1,17}$ = 1.32, $p > 0.05$; 1V3,$F_{1,17}$ = 0,84, $p > 0.05$; 2V3,$F_{1,17}$ = 1.09, $p > 0.05$). Sections 1 and 3 were pruned in this summer and both tended to have higher nitrogen levels during the autumn than section 2.

When the alder is pruned in July it produces a new growth of leaves during August. In late September, when the new growth had ceased, a sample was taken and the soluble nitrogen content measured. The nitrogen level in uncut foliage at this time was 0.47%. That of the new growth was 0.28%. The young leaves produced in late summer therefore contain considerably less soluble nitrogen than mature foliage ($t=32.79, d.f.=16, p < 0.001$).

Figure 165:

Seasonal change in leaf water content of A.glutinosa at East Malling, 1983

(a) LF 125 section 1

(b) WM 110 section 1

(c) WM 110 section 2

(d) WM 110 section 3

Arrows represent date of pruning

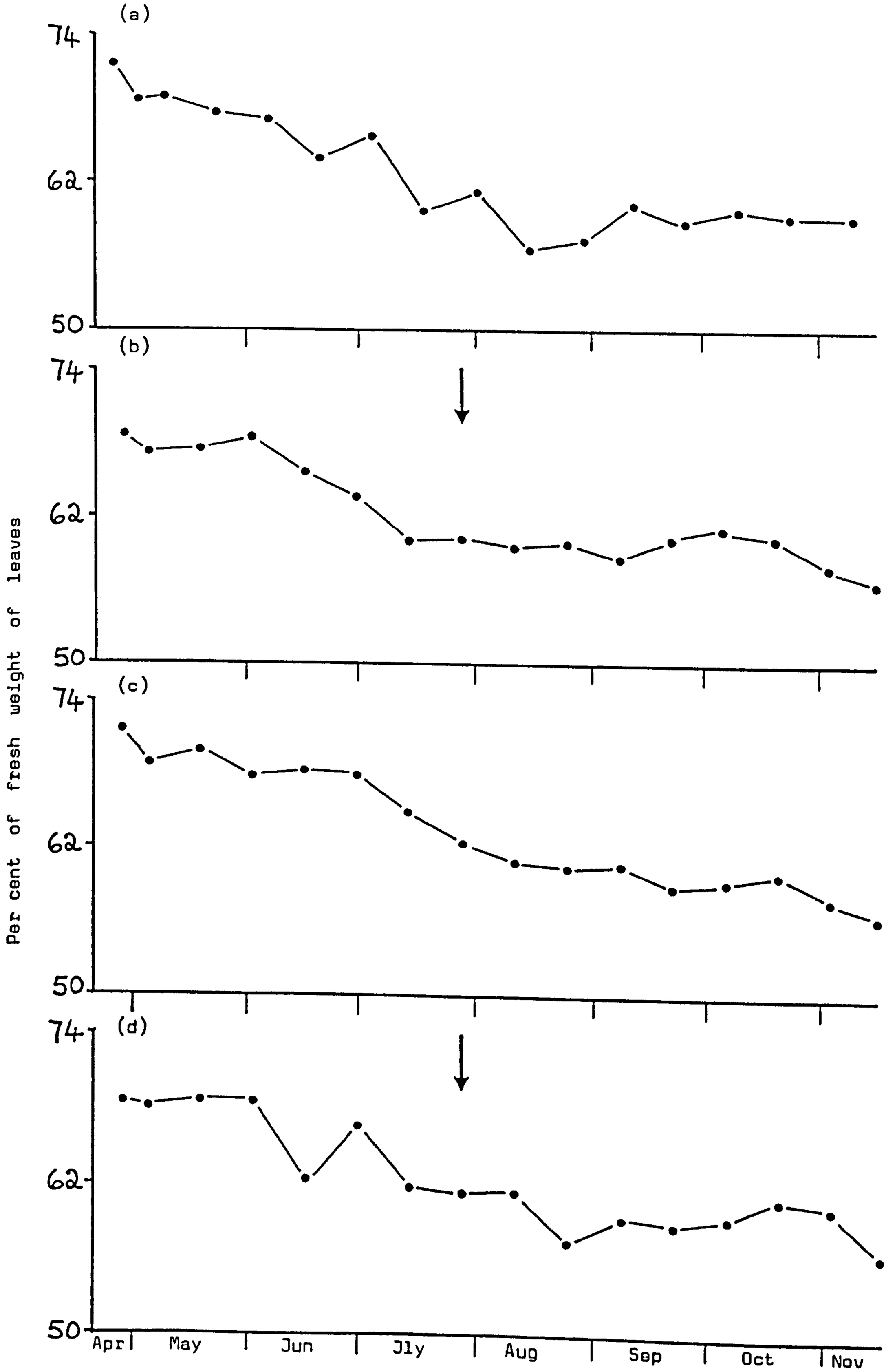

(a)
74
62
50
(b)
74
62
50
(c)
74
62
50
(d)
74
62
50
Per cent of fresh weight of leaves
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 165 cont.

Seasonal change in leaf water content on A.cordata and A.incana at East Malling, 1983.

(d) WM 109 A.cordata

(e) LF 126 A.cordata

(f) LF 126 A.incana

Arrows represent date of pruning

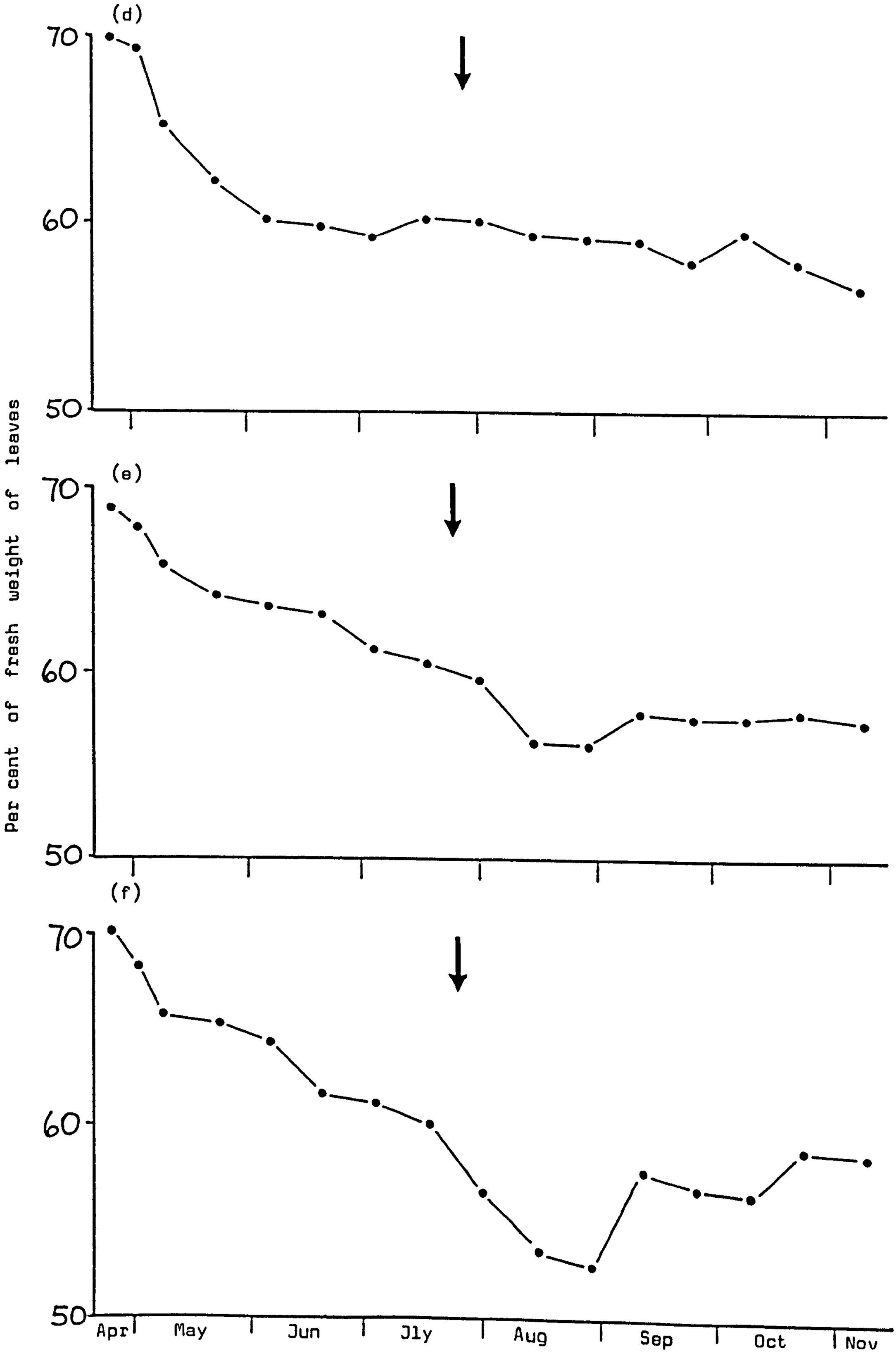

(d)
70
60
50
(e)
70
60
50
(f)
70
60
50
Per cent of fresh weight of leaves
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 166

Seasonal change in foliar soluble nitrogen content of

A.glutinosa at East Malling, 1983

(a) LF 125 section 1

(b) WM 110 section 1

(c) WM 110 section 2

(d) WM 110 section 3

Arrows represent date of pruning

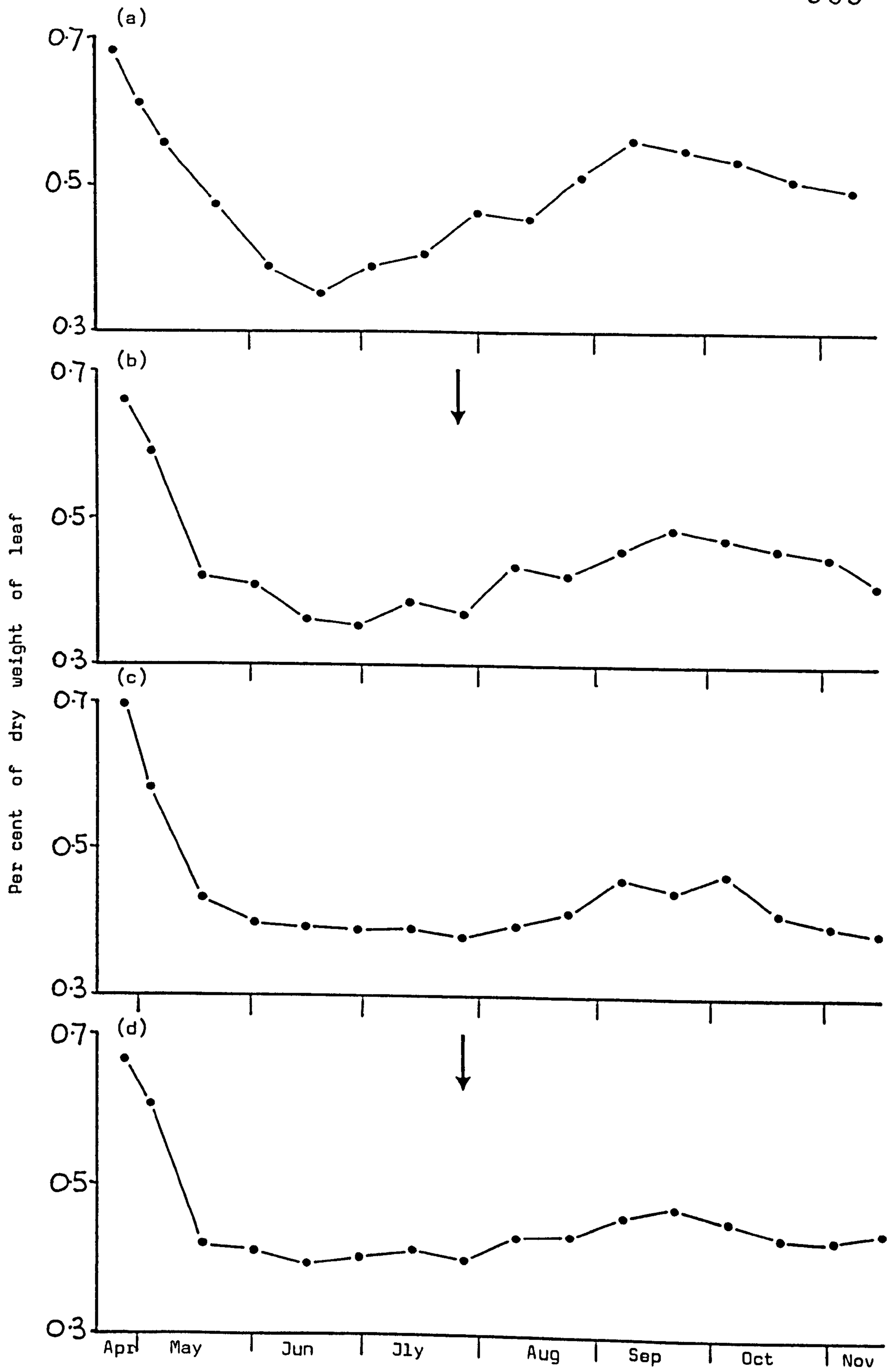

(a)
0·7
0·5
0·3
(b)
0·7
0·5
0·3
(c)
0·7
0·5
0·3
(d)
0·7
0·5
0·3
Per cent of dry weight of leaf
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

Figure 166 cont.

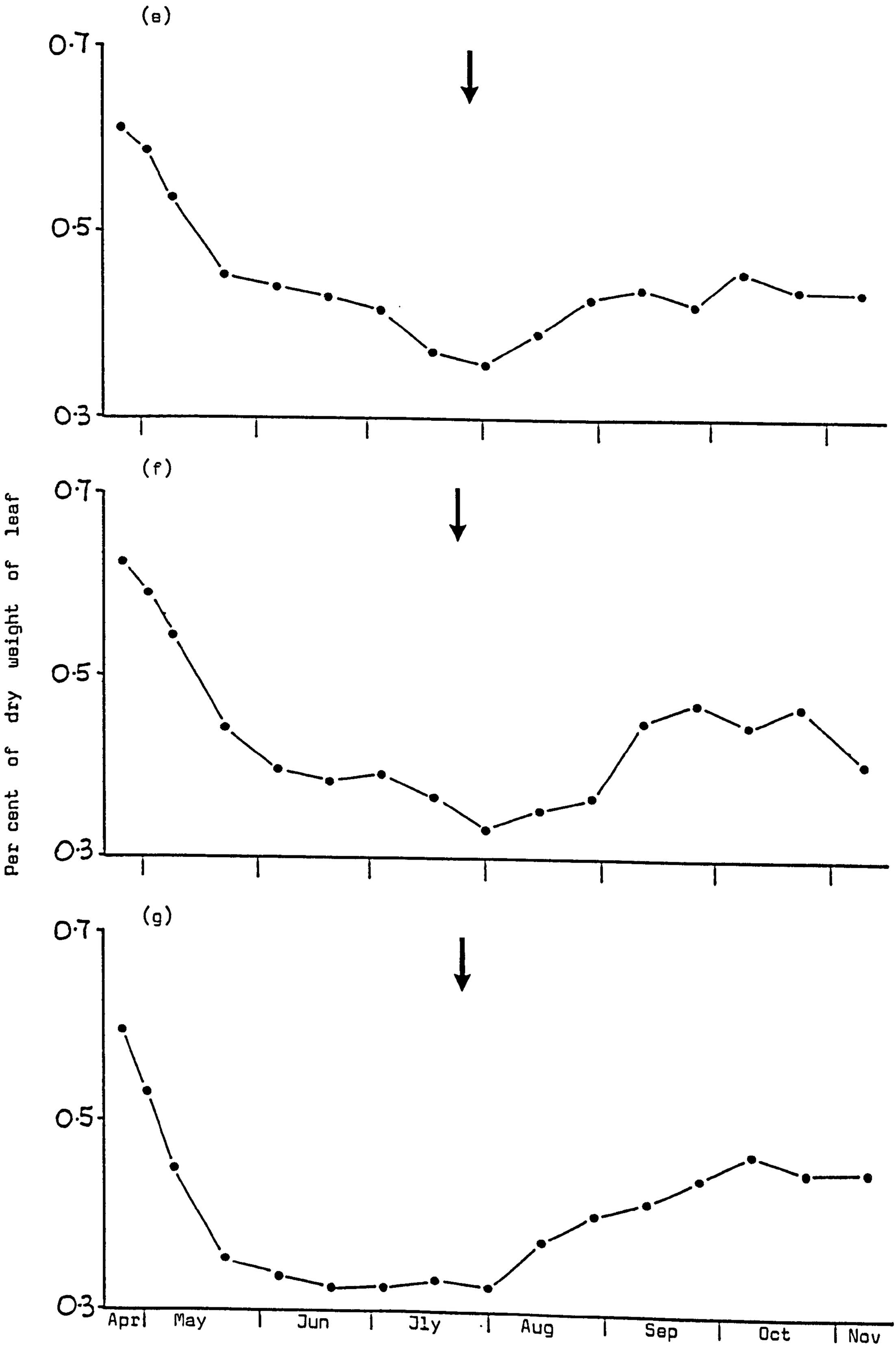
Seasonal change in foliar soluble nitrogen of A.cordata and A.incana at East Malling, 1983

(e) WM 109 A.cordata

(f) LF 126 A.cordata

(g) LF 126 A.incana

Arrows represent date of pruning


(e)
0·7
0·5
0·3
(f)
0·7
0·5
0·3
Per cent of dry weight of leaf
(g)
0·7
0·5
0·3
Apr
May
Jun
Jly
Aug
Sep
Oct
Nov

5.1.4. Discussion

The seasonal decline in leaf water content of alder follows a similar pattern to that described for other trees such as oak (Feeny,1970, Lorriman,1980), sugar maple and yellow birch (Schultz et al,1982). Feeny reported that the water content of oak leaves fell from 70% of fresh weight in May to 50% in mid June thereafter being followed by a gradual decline. Lorriman (1980) found that the water content of oak leaves fell to between 30-47%. Yellow birch (Schultz et al,1982) showed a very gradual decline similar to alder but sugar maple exhibited a much more considerable drop. The alder species in this study all followed very similar patterns of water content. There was no difference between the level of water content in A.glutinosa growing at Lyne and East Malling. At Lyne the trees were growing by the side of a marsh which flooded in winter. At East Malling the soil was considerably drier, but the summer level was still fairly constant at around 59%.

Alders of various species tend to lack synchronous leaf fall and retain green foliage until early winter (Hightshoe,1978). The fact that the leaves remain green suggests that they may retain organic nutrients, especially nitrogenous compounds up to the time of leaf fall (Dawson and Funk,1981). Apple trees lose 40-80% of their leaf nitrogen before leaf fall (Oland,1963) and Viro (1956) reported an average loss of 62% between early August and late September for species of Betula, Populus, Salix and Sorbus. Retranslocated nitrogen in twigs and branches is then readily available for foliar growth the following spring. By mobilizing nitrogen in autumn and storing it for spring, deciduous trees can conserve nitrogen which may be deficient in soils. This is important as in some instances leaves may contain more than 40% of the total nitrogen content in broadleaved trees (Kramer and Kozlowski, 1979) and often more than 30% (Wittwer and Immel, 1980). Alders are able to fix atmospheric nitrogen via root-nodule

symbiosis with actinomycetes of the genus Frankia (Bond,1967). Therefore alders may benefit less from mechanisms of nitrogen conservation having the ability to grow on soils deficient in nitrogen (Dawson et al,1980). Dawson and Funk (1981) attributed the small decrease in total nitrogen in A.glutinosa leaves in autumn to the fact that alder being a nitrogen fixer did not need to conserve nitrogen as much as other trees. Their study of A.glutinosa revealed a very different pattern of nitrogen levels to that reported for such trees as sycamore (Dixon,1963), lime (Dixon,1971c) and oak (Lorriman,1980).

The Illinois alder nitrogen level was 2% dry weight in spring rising to and remaining stable at about 2.8% during summer and falling slightly to 2.5% at leaf fall. The results obtained in the current study differ from this but also from those of other British trees. The alders described in this work showed a drop in soluble nitrogen levels from around 0.6% in spring to around 0.35% in summer, rising again to 0.48% in autumn. In this respect the pattern of abundance is similar to sycamore, lime and oak. A.cordata showed a different seasonal abundance to A.incana and A.glutinosa. The least nitrogen point occurred later in the season, possibly a result of bud burst being later. Leaf fall in this species is also later, not being complete until mid-December. However, the nitrogen content does not drop to such a relatively low level as the other species mentioned. Interpreting graphs can be misleading but table 64 gives a review of the recorded soluble nitrogen contents for a range of trees. Alder soluble nitrogen falls by about 45%, less than that reported for other trees. The unusual pattern followed by total nitrogen in A.glutinosa, reported by Dawson and Funk (1981), may be due to the fact that the Illinois locality in which the alders were sampled was apparently ideal for nitrogen fixation. The high levels of nitrogen in alder foliage throughout the summer has been attributed to the nitrogen-fixing ability of alders (Dawson and Funk,1981; Wittwer and Immel,1980). However, variation was seen to exist between A.glutinosa samples taken from different localities (Dawson et al,1980). Variations

Table 64: Reported soluble nitrogen contents for trees

Tree	Author	peak % N	least % N	% fall
A.pseudoplatanus	Dixon (1963)	0.74	0.24	67.6
T. x vulgaris	Dixon (1971c)	1.5	0.16	89.3
P.padus	Dixon (1971d)	0.66	0.3	54.5
Q.robur	Lorriman (1980)	0.46	0.10	78.3
A.glutinosa	Current work	0.65	0.36	44.1
A.incana	Current work	0.61	0.32	47.9
A.cordata	Current work	0.61	0.35	42.0
A.hybrida	Current work	0.67	0.35	47.8

may be due to soil composition as Bond (1967) reported that molybdenum and cobalt were required for fixation in alder root nodules. East Malling and Lyne may be deficient in these elements relative to silty loams in Illinois or the conditions may not be right for nitrogen fixation in terms of other environmental factors. The fact remains that alders appear to translocate higher levels of soluble nitrogen during summer than other British trees. This is a likely result of their nitrogen-fixing ability.

The effect of this on the aphid population upon the tree is noticeable. Unlike D.platanoidis for example (Dixon, 1963) P.alni can reproduce throughout the summer. The large size of the oviparae in autumn may be a result of the rich food supply available as the nitrogen level being translocated increases.

In a short study such as this effects upon the soluble nitrigen of alder by the aphid population could not be determined. Dixon (1971a) showed that infestations of D.platanoidis on sycamore caused leaves to be shed rich in notrogen in autumn. A similar effect was reported for E.tiliae on lime (Dixon,1971b). Dawson and Funk (1981) reported that only 16% of the nitrogen was removed from the leaves of A.glutinosa in autumn, compared to 40 -50% for trees such as apple (Oland,1963). It was thought that high levels of nitrogen in alders may interfere with the process of leaf senescence. Cytokinin levels in plants that are well supplied with nitrogen are higher than in plants supplied with low levels (Buban, Varga, Tromp, Knegt and Bruinsma,1978). Cytokinins have been demonstrated to delay senescence in the leaves of many plant species (Bonner and Varner, 1976). Therefore, nitrogen retention in the autumnal foliage of alders may explain why the leaves are shed late and green. This does not explain why a considerable amount of alder leaves are shed in summer (Kikuzawa,1980). In that case it was considered that shed leaves were of a protective nature

for later growth and were very small in size. In this study, not only small leaves were shed in summer. This process did not only occur where aphids were abundant (East Malling) being noticed also at Lyne. Thus it is unlikely that a high aphid infestation caused the leaf shedding and the process may have been due to the lowering of the nitrogen content in summer.

The retention of nitrogen helps to explain why alder leaf litter is rich in nitrogenous compounds (Mikola,1958; Turner,Cole and Gessel,1976), this fact having been put to use in soil reclamation and enrichment schemes and forestry (Tarrant,1967). Any effects upon alder induced by P.alni may thus be less noticeable due to the high nitrogen levels caused by fixation. The degree of fixation is likely to vary from year to year and from place to place.

The suggestion of higher nitrogen levels following pruning is interesting but needs further work to establish whether or not this is the case. An important effect of the pruning might be that leaves away from the ends of the branches received more light than those on unpruned sections, possibly increasing the photosynthesis. Pruning may also result in increased photosynthesis as a result of improved water status, such as happens in grand fir (Lopushinsky and Klock,1980). Pruning affecting nitrogen levels has also been reported for Scots pine,Pinus sylvestris L. (Ericsson, Hellqvist,Langström, Larsson and Tenow,1985) and Acacia karoo Hayne (Webb and Moran,1978).

5.2 GROWTH AND REPRODUCTION OF P.ALNI

5.2.1. Introduction

Polymorphism, the development of a number of structurally different forms or morphs is a characteristic of aphids (Hille Ris Lambers,1966). Not only do aphids show variation in form but within these morphs there may be considerable variations in size. Adults of A.fabae for example can weigh from as little as 0.20 mg. to as much as 1.80 mg (Way and Banks,1967). An extensive range in size within and between morphs has been noted for many other species. Small individuals result when aphids develop either under crowded conditions or on mature host plants. The average weight of apterous A.pisum adults was halved when reared at a density of 20 per sq.cm. compared to those reared at 1.25 per sq.cm. (Murdie,1969a). Adults of D.platanoidis are two to four times heavier in spring and autumn (when the food quality of the young or senescing leaves is good) than they are in summer (Dixon 1970b). In addition, aphids reared in crowds on plants of similar physiological age are smaller than those reared in isolation.

Another major cause of size variation in aphids is temperature. All insect populations possess an optimal temperature range for growth, above and below which the innate capacity for increase, determined by the rate of development, fecundity and the length of the reproductive period is lowered. The lower temperature is known as the developmental threshold. This quantity, based on the assumption that the relationship between rate of development and temperature is linear has been estimated for a number of aphid species such as B.brassicae (Hughes,1963), M.evansi and Aphis urticata Gmelin (Perrin,1974) and C.juglandicola (Nowierski, Gutierrez and Yaninek,1983). It is obtained by extrapolating the regression line to the point where development time is zero. The disadvantage of such a procedure is that the development/temperature relationship departs from

linearity towards upper and lower extremes of temperature, as demonstrated by Campbell, Frazer, Gilbert and Mackauer (1974).

The amount of heat required over time for an insect to complete some aspect of its development is considered to be a thermal constant (Andrewartha and Birch,1954). Hughes (1963) devised a physiological time-scale for B.brassicae in the field by integration of the daily temperature in excess of the development threshold. Such a scale is measured in day-degrees and Pruess (1983) reviewed the methods by which these may be calculated.

Temperature affects aphid populations by influencing the rate of development or adult reproduction. In general, increasing temperature results in a shortening of the developmental time and an increase in fecundity (Dean,1974), and a decrease in wet weight and size of appendages (Murdie,1969a). Optimal temperatures for development and size have been established for aphids such as A.pisum (Murdie 1969a) and M.evansi (Perrin,1974).

Aphid size is generally a good indicator of fecundity. A small adult produces fewer and smaller offspring than average (Murdie,1969b, Dixon 1970b , Dixon and Wratten,1971). The relationship between fecundity and adult weight of M.persicae was found to be of a negative exponential rather than a straight line (Kempton,Lowe and Bintcliffe,1980). Taylor (1975) considered that the relation between size and fecundity in A.fabae was indirect and that it was due to reproductive rate and longevity.

Various morphs of aphids have been shown to possess markedly different reproductive strategies. It has long been noted that alatae are less fecund than apterae. This may be a consequence of their small size and the fact that the development and maintenance of wing musculature possibly competes with the development of embryos for the limited nitrogen supply

available. An illustration is provided by Drepanosiphum dixoni H.R.L. in which brachypterous forms (which cannot fly as they lack indirect wing muscles) are 32% more fecund than macropterous alatae (Dixon,1972b). However, alate A.fabae produce as many nymphs in the first few days of adult life as do apterae (Dixon and Wratten, 1971) although they fly and their wing muscles are still functional during this period. Subsequently their reproduction is less than that of apterae. Individuals of A.fabae benefit by being larger and more fecund when feeding in or near aggregates than when alone (Dixon and Wratten,1971) but above a critical density the reproductive rate slows and no further benefit is obtained (Way and Cammell, 1971). Thus it is advantageous for the alata to found a new colony and accentuate reproduction so that the aggregation rapidly builds up to a size whereby the individuals obtain most benefit. In contrast, there is no evidence to suggest that S.avenae or M.dirhodum improve the quality of their food to mutual advantage, nor do they feed in dense aggregations such as A.fabae. Wratten (1977) found that alatae of these two species were less fecund than apterae throughout adult life.

The fecundity of viviparous aphids is dependent on the number of ovarioles (egg tubes) in their ovaries. Ovariole number is dependent on generation and within a generation is independent of size (Wellings,Leather and Dixon, 1980). Those generations with the highest numbers of ovarioles (and therefore potentially most fecund) occur at the beginning of the year when food quality is at its height (Dixon and Dharma,1980, Wellings et al,1980). The seasonal variation in reproductive potential is thus a programmed feature of the aphid life cycle.

The fecundity of aphids observed seasonally is determined by intrinsic factors controlling the number of ovarioles and extrinsic factors such as food quality and temperature which may affect the number of embryos per ovariole and their maturation (Leather and Wellings,1981). It has been

reported that ovariole number may not be intrinsically controlled in Cinara cronartii Tissot and Pepper (Van Rensburg,1981) but may be under the control of some other factor such as nutrition.

Differences in reproductive strategies may be related to differences in ovariole number. In heteroecious aphids, in which ovariole number is not constant within a generation (Wellingset al,1980), increasing the number increases potential fecundity on nutrient-rich hosts. Such a case was shown for A.fabae (Ward, Dixon and Wellings,1983). However, in M.viciae aphids with many ovarioles are less likely to survive to maturity on poor hosts than those with a lesser number (Ward,Wellings and Dixon,1983). An aphid on a poor host is unlikely to experience improvement in the food quality in its lifetime. There is little to gain by postponing reproduction therefore the largest embryos are matured and the smallest resorbed (Ward and Dixon,1982). Those with a small number of ovarioles may survive to produce at least some offspring which may experience improved conditions. Recovery may be slow; in A.fabae (Dixon and Wratten,1971) it can take 3 - 4 generations for size and fecundity to be recovered.

Compared to laboratory investigations, direct measurements of aphid growth and reproductive rates in the field have rarely been attempted. Examples include work with D.platanoidis (Dixon 1970b,1975), T.tuberculatus (Lorriman,1980) and C.juglandicola (Nowierski et al,1983). Most workers have favoured an indirect method, either estimating reproductive rates from census data (Hughes,1963) or by recording rates at known temperatures and then generalizing to field conditions (Perrin,1974).

In this section, the growth and reproduction of P.alni in the field and under controlled conditions in the laboratory are reported.

5.2.2. Materials and methods

All aphids were reared in clip cages of the type described by Noble (1958). Dixon (1977) stated that caging may afford aphids shelter and protection and thus affect reproductive rates. Perrin (1974) compared the fecundity of M.evansi on excised leaves and in cages on intact leaves. No differences were found and so with this reservation in mind, cages were employed.

Small pieces of twigs bearing eggs were collected in early April and placed in petri dishes on a base of slightly moistened filter paper. The dishes were placed in an outside shed and examined daily. Fundatrices were weighed within 12 hours of hatching. They were transferred to leaves in the field or to saplings in constant temperature rooms. Experiments involving alate production reported earlier made us of petioles banded with 'Oecotak' in the latter part of April. Leaves of similar ages were chosen in this experiment and cages applied. All leaves were virtually fully expanded so that minimal damage occurred. Aphids were caged from birth to provide uniformity of technique.

Cages were inspected daily and the day on which the adult became mature recorded. The day on which reproduction commenced was noted thus giving an estimate of the pre-reproductive delay. This is likely to be somewhat inaccurate. Examining cages only daily could result in an error of up to 23 hours. Aphids were weighed on the day they became adult. At East Malling the adults were transferred to small glass vials and transported to the laboratory in a cool box, where they were weighed on a Cahn 26 microbalance. At Lyne, aphids were transported to Imperial College field station, Silwood Park, and weighed on a Beckman LM500 microbalance. The starvation period from removal to replacement was less than 2 hours in all cases. The weight of the offspring produced on the second day

of reproduction was recorded and thereafter cages were examined every three days and all offspring produced counted and removed. Experiments in the field were continued until the aphids died. Those under constant temperatures of $15^{o}C \pm 1.0^{o}C$ and $20^{o}C \pm 1.1^{o}C$ were continued for 28 days and at $10^{o}C \pm 1.6^{o}C$ for the duration of development time plus the pre-reproductive time as this was longer. All growth room experiments were carried out in a light regime of 16h day. Only aphids which survived for 28 days were included in the analyses of fecundity and weight. Successive generations were reared throughout the summer, starting in mid April, May, June, July, August and September.

Experiments were started at each temperature simultaneously with those in the field. Offspring produced by each generation were used to start the next in the field and field offspring were used to start each experiment indoors. Saplings of A.glutinosa, A.cordata and A.incana were used indoors and at East Malling aphids were reared upon LF125 (A.glutinosa) and LF126 (A.cordata and A.incana). In addition, aphids were reared during the summers of 1983 and 1984 on WM110 and their weights recorded when adult, thus giving an indication of adult weight attained throughout the season. At Lyne the species used were A.glutinosa, A.incana and A.hybrida.

Saplings for use in the growth rooms were kept outside and brought into the rooms on the day before the experiment started. Three saplings were used for each generation. At $20^{o}C$ aphids were reared on saplings which were brought indoors in mid March before bud burst and maintained in the growth room in addition to those brought in for each experiment. All saplings were potted in John Innes number 2 compost and kept for a year to become established, in London University's Botanic Garden, Egham, Surrey.

At least 15 aphids were reared in each experiment except on A.incana where mortality in the field was often high. All aphids reared at

constant temperatures were apterous. In the field alatae of generations 2 and 3 were reared on A.glutinosa. At 20°C, aphids were reared singly and in crowds to investigate the effect of crowding on size. The relationship between the size of the mother and the size of her offspring was also examined at this temperature.

The mean relative growth rates for all individuals were calculated using the formula:

$$M.R.G.R. \quad (mg^{-1}mg^{-1}day^{-1}) = \frac{\ln W2(mg) - \ln W1\ (mg)}{t_2 - t_1}$$

where W1 and W2 are the weights at birth and maturity respectively and $(t_2 - t_1)$is the time taken to develop from birth to adulthood (development time). The formula is derived from an integral expression based on relative growth rate $(1/W = dw/dt)$. This does not involve assumptions about the form of the growth curve (Radford,1967) and comparison between species is therefore possible.

The intrinsic rate of increase (rm) was calculated using the formula developed by Wyatt and White (1977):

$$rm = 0.74\ (\ln Md/Td)$$

where Md is the number of nymphs produced over a period of time equal to the prereproductive period (Td) and 0.74 is a constant. Laboratory measurements of rm have been useful in comparing the reproductive potentials of different morphs of one species (Dixon and Wratten,1971) or of different species (Dean, 1974). However, in estimating rm it is assumed that the population has achieved a stable age distribution and as this rarely occurs (Carter et al,1978) estimates of this parameter are inapplicable to populations in the field. In these experiments estimates of rm were obtained for the three alder species at the three temperatures concerned.

The relationship between rm and MRGR was investigated in a comparison with the work of Leather and Dixon (1984). In that study a very close relationship was found for R.padi.

Aphids were sampled randomly in the field throughout the period of abundance during 1982 and 1983. They were taken from the unsampled faces of LF125 and WM110, weighed, dissected and the number of embryos with pigmented eyes recorded. This gives an indication of the reproductive potential of the aphid (Dixon, 1963; 1976b). A number of aphids were reared on LF125, dissected and the number of embryos counted. The relationships between adult weight, total embryo count and pigmented eye embryo count were examined.

In these experiments three different microbalances were used. To determine whether the readings obtained were comparable a sample of pieces of aluminium foil was wighed on each of the balances. The mean weights recorded were as follows:

balance	mean weight/mg	t value
Cahn, Queen Elizabeth College (C.T. room work)	1.439 ± 0.006	(-1.516) N.S. (- 1.891)
Cahn, East Malling	1.427 ± 0.005	(-1.385) N.S.
Beckman, Lyne	1.444 ± 0.007	(n = 12)

The balances gave very similar readings thus results from each locality may be directly comparable.

5.2.3. Results

(a) Lyne

The first generation of aphids on A.incana suffered 100% mortality. Subsequent generations were reared in large numbers to determine whether P.alni could be reared on this tree or whether mortality was due to starvation. Examination of cages revealed that many aphids reached 2nd or 3rd instar before death so some feeding took place. Although mortality was high in the summer generations, enough aphids became mature for comparisons to be made with those reared on A.glutinosa and A.hybrida, where mortality was considerably lower. In the fifth generation mortality on A.incana was again 100% and no results were obtained.

Analysis of variance revealed that there were changes in the development time and adult weight of aphids reared on A.glutinosa and A.hybrida over the season (table 65). Weight and development time were greatest in the first generation, born in mid April and least in the fourth generation, born in mid July. (For development time, $F = 267.70, p < 0.001$ and for weight, $F = 117.41$, $p < 0.001$). There were no differences between the weights or development times of each generation reared on A.glutinosa or A.hybrida (development time, $F = 5.67, p > 0.05$, weight, $F = 0.027, p > 0.05$). The generations reared on A.incana showed a similar trend. The first generation were most fecund, producing an average of 83.2 nymphs per female on A.glutinosa and 79.4 nymphs on A.hybrida. Summer generations produced considerably fewer with a rise again in the fifth generation (table 65) ($F = 95.26$, $p < 0.001$) but there were no differences between generations on A.glutinosa and A.hybrida ($F = 0.909$, $p > 0.05$).

Each generation lived on average for a very similar amount of time. Aphids on A.incana lived for shorter periods of time than on A.glutinosa or

Table 65: Growth and reproduction of P.alni on three alder species at Lyne, 1983

Gen.	Number reared	Nymphal mortality %	Development time/days	Adult weight mg	Fecundity	Adult lifespan days	M.R.G.R. mg mg^{-1} day^{-1}
(a) A.glutinosa							
1	19	17.4	35.8 ±0.3	0.381 ±0.016	63.2 ± 4.9	49.4 ± 1.1	0.089 ±0.001
2	24	4.0	20.5 ± 0.2	0.240 ±0.013	60.2 ± 3.8	53.4 ± 0.9	0.133 ±0.002
3	25	7.4	20.4 ± 0.1	0.169 ±0.007	56.4 ± 3.5	46.4 ± 0.8	0.118 ±0.001
4	27	0	16.4 ± 0.09	0.161 ±0.004	40.1 ± 1.6	47.7 ± 1.1	0.145 ±0.002
5	24	11.1	18.2 ± 0.1	0.210 ±0.009	57.4 ± 2.1	55.7 ± 0.9	0.145 ±0.002
(b) A.hybrida							
1	17	15.0	37.9 ± 4.1	0.370 ±0.017	69.4 ± 5.1	48.6 ± 4.1	0.084 ±0.001
2	20	16.7	22.1 ± 3.1	0.252 ±0.014	63.4 ± 4.3	50.3 ± 4.4	0.117 ±0.001
3	21	19.2	21.1 ± 2.0	0.174 ±0.006	52.4 ± 2.1	50.3 ± 1.2	0.116 ±0.002
4	18	14.3	16.0 ± 0.9	0.141 ±0.008	40.4 ± 1.1	48.3 ± 2.1	0.140 ±0.002
5	25	24.2	19.4 ± 1.1	0.230 ±0.009	55.2 ± 3.6	51.3 ± 2.2	0.142 ±0.003
(c) A.incana							
1		100					
2	14	67.4	23.1 ± 1.6	0.199 ±0.011	43.1 ± 2.6	39.1 ± 3.1	0.109 ±0.001
3	18	73.1	22.6 ± 1.4	0.168 ±0.012	49.1 ± 3.1	33.3 ± 4.1	0.107 ±0.001
4	12	78.6	17.1 ± 1.3	0.127 ±0.004	32.3 ± 2.3	36.4 ± 2.1	0.125 ±0.002
5		100					

A.hybrida and as a result their fecundity was lower.

The mean relative growth rate was lowest for the first generation; a consequence of the length of development time early in the season (table 65). It was greatest for late summer generations when development time was relatively short.

(b) East Malling

A.cordata bore no expanded leaves in mid April and thus no fundatrices could be reared upon this species. Colonization of buds by fundatrices was attempted but all individuals died. Mortality of nymphs was high on A.incana throughout the season and also on A.cordata.

(i) A.glutinosa

The development time of apterae was greatest for the first generation (33 days) decreasing until the shortest time was recorded (16 days) for the aphids of the fourth generation, born in mid July (table 66). The teneral adult weight followed a very similar trend, decreasing from 0.345 mg in April to 0.145 mg in early August, subsequently increasing. The first generation was most fecund, producing an average of 68 nymphs per female, but this was not significantly greater than the second generation ($t = 1.46, d.f.=41, p>0.05$). Fecundity fell in succeeding generations to reach a minimum of 34 nymphs per female for those adults of the fourth generation, born in mid July and reproducing during August. The changes in fecundity were associated with changes in the adult life span, which followed a very similar trend. The weight of the offspring produced also followed a seasonal trend. Fundatrices hatching from eggs were largest, weighing 0.0157 mg. significantly larger than those produced by fourth generation adults which weighed 0.0132 mg ($d=3.22, p<0.001$).

Table 66: Growth and reproduction of apterae on A.glutinosa, East Malling, 1984. Values tabulated are means ± standard error.

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult Weight mg	Fecundity	Adult lifespan days	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}
1 April	20	13.0	33.2 ± 0.8	0.345 ±0.014	67.9 ± 2.1	50.8 ± 0.6	0.0158 ±0.0006	0.089 ±0.004
2 May	23	23.3	23.9 ± 0.7	0.266 ±0.007	64.2 ± 1.5	52.6 ± 1.1	0.0143 ±0.0005	0.121 ±0.003
3 June	26	10.3	20.3 ± 0.4	0.178 ±0.003	58.1 ± 1.1	49.8 ± 1.08	0.0139 ±0.0004	0.132 ±0.004
4 July	28	3.4	16.0 ± 0.4	0.145 ±0.003	33.8 ± 0.8	36.4 ± 0.8	0.0133 ±0.0002	0.147 ±0.003
5 August	33	5.7	16.9 ± 0.3	0.159 ±0.005	50.5 ± 1.0	62.3 ± 0.9	0.0132 ±0.0002	0.145 ±0.003
6 September	31	12.9	18.4 ± 0.6	0.253 ±0.007	51.9 ± 1.4	56.8 ± 1.1	0.0138 ±0.0002	0.158 ±0.004
7 September								
Oviparae	25	11.8	24.8 ± 0.6	0.484 ±0.011			0.0149 ±0.0001	0.140 ±0.004
Males	19	7.1	29.4 ± 0.4	0.144 ±0.004			0.0149 ±0.0001	0.077 ±0.004

The lowest mean relative growth rate was recorded for the fundatrix generation at 0.089 mg mg^{-1} day^{-1}. As a consequence of the shortening development time, this quality rose throughout the summer, the highest rate (0.158) being recorded for the sixth generation, born in early September where the development time was relatively short (18 days) and aphids relatively large (0.253 mg).

The teneral weight of alatae in generation 2 (0.133 mg) was considerably lower than the average weight attained by apterae (0.266 mg) ($d = 8.74$, $d.f.=29$, $p < 0.001$) and that of alatae in the third generation (0.115 mg) was also significantly smaller than the 0.178 mg attained by apterae ($t = 11.27$, $d.f.=42$, $p < 0.001$) (table 67). Alatae of the second generation were larger than those of the third ($t = 2.29$, $d.f.= 31$, $p<0.05$). There were no differences in development time of alatae and apterae in generation 2 ($t = 0.77$, $d.f.=36$, $p > 0.05$) or generation 3 ($t=1.85$, $d.f.=42$, $p > 0.05$). Alatae of generation 2 took an average of 24.7 days to develop and those of generation 3, 20.7 days; a significant difference ($t = 4.06$, $d.f.=31$, $p < 0.001$).

In both generations the average number of offspring produced per female was considerably less for alatae. Apterae of generation 2 produced 64.2 nymphs per female whereas alatae produced 49.9 ($t = 4.44$, $d.f.=36$, $p < 0.001$). Third generation apterae produced 58.1 nymphs per female, significantly more than the 33 per alate female ($t = 7.10$, $d.f.=42$. $p < 0.001$). Second generation alatae were more fecund than third generation individuals ($t = 4.45$, $d.f.= 31$, $p < 0.001$).

Due to the lower weight of alatae, the mean relative growth rate achieved by apterae was higher. In the second generation that for apterae was 0.1205 mg $mg^{-1}day^{-1}$, greater than the 0.0903 mg $mg^{-1}day^{-1}$ achieved by alatae ($t = 6.79$, $d.f.=36$, $p < 0.001$). In the third generation that for

Table 67: Growth and reproduction of alatae on A.glutinosa LF 125, East Malling, 1984

Generation	Number reared	Nymphal mortality %	Development time/days	Adult Weight mg	Fecundity	Adult lifespan days	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}
2	15	10.3	24.7 ± 0.7	0.133 ±0.006	49.9 ± 2.1	48.7 ± 1.0	0.0143 ±0.0001	0.090 ±0.003
3	18	13.9	20.7 ± 0.7	0.115 ±0.005	33.0 ± 3.0	51.4 ± 0.9	0.0139 ±0.0003	0.102 ±0.003

Table 68 Growth and reproduction of apterae on LF126, 1984 (means ± standard error)

Generation	Number reared	Nymphal mortality %	Development time/days	Adult Weight mg	Fecundity	Adult lifespan days	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}
A: A.cordata								
1								
2	15	42.3	25.7 ± 0.7	0.270 ±0.007	49.1 ± 1.4	44.3 ± 1.3	0.0141 ±0.0003	0.113 ±0.004
3	17	52.7	21.6 ± 0.6	0.236 ±0.003	43.6 ± 1.0	39.2 ± 0.8	0.0138 ±0.0001	0.127 ±0.004
4	24	64.2	17.5 ± 0.4	0.157 ±0.004	38.5 ± 0.8	34.2 ± 0.7	0.0133 ±0.0002	0.147 ±0.004
5	21	41.7	18.3 ± 0.5	0.132 ±0.005	33.5 ± 0.9	31.4 ± 0.8	0.0132 ±0.0002	0.123 ±0.004
6	20	50.0	19.5 ± 0.5	0.230 ±0.009	46.4 ± 1.3	48.5 ± 1.1	0.0138 ±0.0002	0.140 ±0.004
7 Ov	19	36.7	25.2 ± 0.5	0.434 ±0.012			0.0146 ±0.0001	0.130 ±0.004
M	24		31.3 ± 0.6	0.136 ±0.009			0.0146 ±0.0001	0.071 ±0.002
B: A.incana								
1	14	66.7	34.3 ± 1.0	0.306 ±0.011	60.4 ± 1.6	40.3 ± 1.1	0.0158 ±0.0003	0.077 ±0.004
2	13	70.5	25.9 ± 1.1	0.269 ±0.008	44.2 ± 1.4	40.1 ± 1.1	0.0141 ±0.0004	0.111 ±0.004
3	10	80.0	21.5 ± 0.8	0.169 ±0.005	31.1 ± 1.3	33.6 ± 0.9	0.0138 ±0.0001	0.101 ±0.006
4	18	61.7	17.8 ± 0.4	0.137 ±0.004	25.1 ± 0.7	30.1 ± 0.8	0.0133 ±0.0004	0.125 ±0.004
5	15	75.0	17.4 ± 0.4	0.160 ±0.005	45.1 ± 1.3	48.6 ± 1.2	0.0132 ±0.0002	0.136 ± 0.004
6	16	66.7	20.3 ± 0.6	0.247 ±0.011	44.5 ± 1.5	46.4 ± 1.3	0.0138 ±0.0002	0.138 ±0.004
7 Ov	23	50.0	24.1 ± 0.6	0.419 ±0.015			0.0144 ±0.0001	0.123 ±0.002
M	14		31.4 ± 0.7	0.123 ±0.008			0.0144 ±0.0001	0.070 ±0.003

apterae was 0.132 $mg^{-1}mg^{-1}day^{-1}$, significantly higher than the 0.102 $mg^{-1}mg^{-1}day^{-1}$ of alatae ($t = 5.56, d.f. = 42, p < 0.001$).

(ii) A.incana and A.cordata

The growth and reproduction of P.alni on these species followed similar trends to those described on A.glutinosa (table 68). In the first generation, fundatrices on A.incana took as long to develop as on A.glutinosa ($t = 0.97$, d.f.=32, $p > 0.05$), but were of a lesser weight ($t = 2.33$, d.f.=42, $p < 0.05$) and lived for a shorter period of time ($t = 10.30$, d.f.=42. $p<0.001$) and consequently produced fewer offspring ($t = 2.64$, d.f.=42, $p < 0.05$). The relative growth rate on A.glutinosa was greater than on A.incana ($t = 2.38$, d.f.=42, $p < 0.05$). The differences in growth of apterae reared on the three alder species are summarized in table 69. Within each generation there were only minor differences in the development time on each species. Apterae reared on A.glutinosa and A.incana were similar in weight in each generation after the first. Those reared on A.cordata were larger in the third generation but the lowest weight attained on this species was in the fifth generation, as opposed to the fourth on A.glutinosa and A.incana (table 69). Adults reared on A.cordata were therefore significantly smaller in the fifth generation. With few exceptions, aphids lived for a longer time on A.glutinosa than on A.incana or A.cordata and produced more offspring on A glutinosa. In the fourth generation when aphids were smallest and least fecund on A.glutinosa and A.incana those on A,cordata were larger more fecund and lived longer than on A.incana.

A summary of the differences in growth rate is presented in table 70. Aphids achieved higher relative growth rates on A.glutinosa than on A.incana in every generation except the second and fifth. Only in the fifth and sixth generations was the growth rate higher on A.glutinosa compared with

Table 69: Summary of the statistical differences between the growth and reproduction of P.alni generations on A.glutinosa, cordata and incana (all means tested by 'students' t tests)

	Development time/days	Adult weight mg	Adult lifespan days	Offspring produced	Development time/days	Adult weight mg	Adult lifespan days	Offspring produced	Development time/days	Adult weight mg	Adult lifespan days	Offspring produced
Generation:		1				2				3		
glutinosa v. cordata					-1.74 N.S.	-0.39 N.S.	4.83 ***	6.94 ***	-1.73 N.S.	-11.90 ***	6.90 ***	9.19 ***
glutinosa v. incana	0.97 N.S.	2.33 *	10.30 ***	2.64 *	-1.60 N.S.	-0.27 N.S.	7.42 ***	8.84 ***	-0.68 *	1.56 N.S.	8.52 ***	13.84 ***
cordata v. incana					-0.16 N.S.	0.09 N.S.	2.42 *	2.46 *	0.09 N.S.	12.26 ***	3.73 ***	7.63 ***
Generation		4				5				6		
glutinosa v. cordata	-2.51 *	-2.39 *	1.95 N.S.	-4.19 ***	-2.46 *	3.25 **	28.63 ***	11.92 ***	-1.25 N.S.	2.03 N.S.	5.09 ***	2.67 *
glutinosa v incana	-2.63 *	1.62 N.S.	5.53 ***	7.58 ***	-0.96 N.S.	-0.14 N.S.	10.81 ***	0.94 N.S.	-2.01 N.S.	0.64 N.S.	5.72 ***	3.13 **
cordata v. incana	-0.53 N.S.	3.46 **	3.87 ***	12.61 ***	1.31 N.S.	-3.88 ***	-12.44 ***	-7.88 ***	-1.30 N.S.	-1.60 N.S.	1.21 N.S.	0.90 N.S.

Note: ***:$p \leqslant 0.001$; ** $p \leqslant 0.01$; * $p \leqslant 0.05$

Table 70: Differences in the growth rate of apterous P.alni on A.glutinosa, cordata and incana during 1984 at East Malling

Generation:	1	2	3	4	5	6
glutinosa v. cordata		1.63	0.85	0	4.64	3.04
		N.S.	N.S.	N.S.	***	**
glutinosa v. incana	2.07	2.00	4.19	4.40	1.49	2.76
	*	N.S.	***	***	N.S.	**
cordata v. incana		0.35	3.73	3.89	-2.33	0.35
		N.S.	***	***	*	N.S.

Note: ***:$p \leqslant 0.001$; ** $p \leqslant 0.01$; * $p \leqslant 0.05$

A.cordata. The rate on A.cordata was most dissimilar from that on A.incana in midsummer.

Oviparae reared on A.glutinosa took the same amount of time to develop as those on A.cordata ($t = 0.49$, d.f.=42. $p > 0.05$) and A.incana ($t = 0.82$, d.f.= 46, $p > 0.05$). However, they were heavier at maturity on A.glutinosa (v.cordata, $t = 3.07$, d.f.= 42, $p < 0.001$; v.incana, $t = 3.49$, d.f.=46, $p < 0.01$). Those reared on A.cordata were similar in weight to those on A.incana ($t = 0.77$, d.f.=40, $p > 0.05$). Dissection of these oviparae revealed differences in the egg content. Those on A.glutinosa contained an average of 14.86 eggs, significantly more than the 8.49 in those on A.cordata ($t = 9.66$, d.f.=42, $p < 0.001$), and 8.88 on A.incana ($t = 8.74$ d.f.=46, $p < 0.001$). There was no difference between the egg content of these individuals reared on A.cordata and A.incana ($t = 1.41$, d.f.=40, $p > 0.05$). The mean relative growth rate on A.glutinosa was similar to that on A.cordata ($t = 1.73$, d.f.=42 $p > 0.05$) but greater than that on A.incana ($t = 3.30$, d.f. = 46. $p < 0.001$). The rate achieved on A.cordata was similar to that on A.incana ($t = 1.39$, d.f.=40, $p > 0.05$).

The weights attained by batches of aphids reared successively throughout the summers of 1983 and 1984 are depicted in fig.167 a,b. Split lines were fitted to the data using the method described by Perry (1982). Weights followed a similar seasonal pattern in both years with minimum weights being attained during August in each year. In 1983, the calculated value of c, the intersection of the regression lines produced the date of August 11th. In 1984 this date was August 17th.

Allowing for inaccuracies in such extrapolation, the minimum weight of aphids becoming adult occurred at a similar time in both years. The development time of aphids born in late July in 1983 was 12 days, whereas at the same time in 1984 this was 16 days. Thus the smallest aphids were

Figure 167

Seasonal change in adult weight attained in P.alni on A.glutinosa.

Fitted split lines:

(a)

down: $y = -0.004x + 0.390$

$r = -0.9541$, d.f. = 4, $p < 0.01$

up: $y = 0.004x - 0.319$

$r = 0.9764$, d.f. = 4, $p < 0.001$

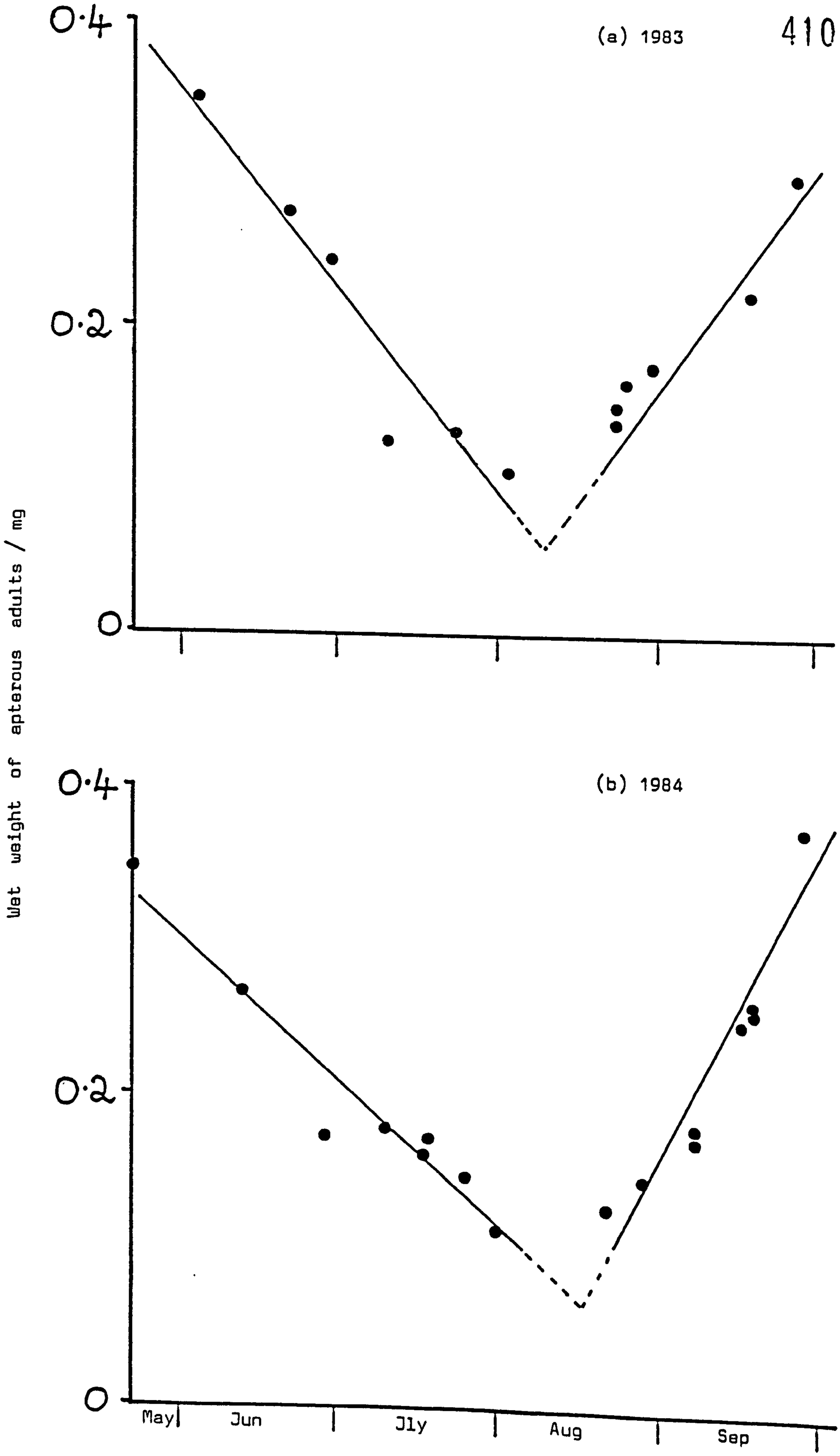
(b)

down: $y = -0.003x + 0.328$

$r = -0.9619$, d.f. = 6, $p < 0.001$

up: $y = 0.006x - 0.471$

$r = 0.9026$, d.f. = 6, $p < 0.01$


(a) 1983
(b) 1984
Wet weight of apterous adults / mg
0·4
0·2
0
May
Jun
Jly
Aug
Sep

born at a similar time in both years. The hypothetical value d of the lowest weight attained in each year was 0.055mg in 1983 and 0.069mg in 1984. In both years the minimum weight attained occurred after the date of peak population density, this being July 21st in 1983 and August 2nd in 1984.

(c) Constant temperature studies

Mortality was considerably less on A.cordata and A.incana at constant temperatures than it was in the field. More nymphs tended to die on A.cordata and A.incana at 10°C. The results for aphids reared at 10°C 15°C and 20°C on A.glutinosa are given in tables 71-74, for A.cordata in tables 75-77 and for A.incana in tables 78-80. All values tabulated are means with attached standard errors.

There was no difference between the development time of each generation when reared on A.glutinosa saplings, whether kept indoors or outdoors (tables 73 and 74) ($F6_{16} = 2.86$, $p > 0.05$) at 20°C. However, the weights of each generation showed a seasonal trend on saplings kept outside, similar to that observed in the field. When reared on saplings maintained in the room, the weight of the fundatrix generation (0.212mg) was not significantly different from that of the fifth generation (0.204mg), the lowest weight recorded ($t=1.02, d.f.=33, p > 0.05$). On saplings kept outside, the fundatrices (0.260mg) were significantly heavier than the smallest aphids reared, of the third generation (0.182mg; $t = 7.21, d.f.=32, p < 0.001$). At 10°C and 15°C (tables 71 and 72) where saplings were maintained in the rooms, there was a suggestion of a seasonal trend in weight, but there were no differences between the largest and smallest weights (10°C: $t=1.40$, $d.f.=29$, $p > 0.05$; 15°C: $t=1.61, d.f.=34$, $p > 0.05$). Fecundity was similar between generations at each temperature, but at 20°C on outdoor-kept saplings a seasonal trend occurred, a likely result of the associated

Table 71: Growth and reproduction of apterous P.alni on A.glutinosa at 10°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	15	25	34.8 ± 1.2	0.282 ±0.008	26.8 ± 0.9	0.0155 ±0.0006	0.084 ±0.001	0.064 ±0.001
2 May	16	20	34.3 ± 1.4	0.289 ±0.014	25.5 ± 0.7	0.0144 ±0.0004	0.087 ±0.001	0.064 ±0.0008
3 June	19	5	35.1 ± 1.4	0.270 ±0.013	24.1 ± 0.6	0.0142 ±0.0003	0.083 ±0.001	0.063 ±0.0009
4 July	16	20	34.2 ± 1.1	0.264 ±0.01	24.8 ± 0.8	0.0136 ±0.0004	0.082 ±0.0008	0.062 ±0.0009
5 August	19	5	34.8 ± 1.3	0.271 ±0.009	26.1 ± 0.9	0.0145 ±0.0005	0.083 ±0.0009	0.063 ±0.0008
6 September	18	10	34.4 ± 1.1	0.280 ±0.013	24.0 ± 0.9	0.0142 ±0.0004	0.084 ±0.002	0.064 ±0.0009
7 Oviparae September	14	30	34.6 ± 1.5	0.300 +0.017		0.0143 +0.0004	0.088 +0.002	

Table 72: Growth and reproduction of apterous P.alni on A.glutinosa at 15°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	19	5	19.8 ± 0.36	0.264 ±0.009	58.7 ± 1.1	0.0160 ±0.0007	0.142 ±0.002	0.130 ±0.0007
2 May	18	10	19.7 ± 0.31	0.269 ±0.011	59.2 ± 1.8	0.0142 ±0.0004	0.143 ±0.004	0.128 ±0.001
3 June	19	5	19.3 ± 0.24	0.258 ±0.010	58.8 ± 1.1	0.0148 ±0.0003	0.148 ±0.003	0.128 ±0.0007
4 July	17	15	19.9 ± 0.39	0.247 ±0.008	58.4 ± 1.7	0.0135 ±0.0004	0.136 ±0.001	0.120 ±0.001
5 August	19	5	19.8 ± 0.40	0.256 ±0.012	57.4 ± 1.4	0.0139 ±0.0003	0.142 ±0.003	0.126 ±0.001
6 September	18	10	19.1 ± 0.35	0.261 ±0.011	60.4 ± 1.9	0.0139 ±0.0004	0.150 ±0.002	0.132 ±0.004
7 Oviparae September	19	5	19.6 + 0.33	0.285 +0.013		0.0144 +0.0005	0.153 +0.004	

Table 73: Growth and reproduction of apterous P.alni on A.glutinosa saplings kept at 20°C throughout the season

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	16	20	13.8 ± 0.38	0.212 ±0.006	55.7 ± 2.1	0.0157 ±0.0004	0.194 ±0.002	0.160 ±0.002
2 May	17	15	13.2 ± 0.17	0.207 ±0.005	56.3 ± 2.3	0.0144 ±0.0005	0.191 ±0.004	0.165 ±0.003
3 June	20	0	13.8 ± 0.29	0.214 ±0.005	57.1 ± 2.2	0.0141 ±0.0005	0.193 ±0.004	0.164 ±0.002
4 July	20	0	13.5 ± 0.23	0.219 ±0.007	56.1 ± 2.0	0.0137 ±0.0004	0.198 ±0.004	0.165 ±0.003
5 August	19	5	13.6 ± 0.31	0.204 ±0.005	51.8 ± 2.1	0.0135 ±0.0004	0.188 ±0.004	0.160 ±0.002
6 September	20	0	13.2 ± 0.11	0.216 ±0.007	51.5 ± 2.2	0.0141 ±0.0005	0.194 ±0.004	0.160 ±0.003
7 Oviparae September	20	0	13.9 ± 0.31	0.219 ±0.009		0.0144 ±0.0005	0.196 ±0.005	

Table 74: Growth and reproduction of apterous P.alni on A.glutinosa saplings kept outdoors, at 20°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult Weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	16	20	13.9 ± 0.36	0.260 ±0.009	60.7 ± 2.1	0.0156 ±0.0006	0.209 ±0.003	0.169 ±0.003
2 May	17	15	13.8 ± 0.24	0.239 ±0.008	54.5 ± 1.8	0.0144 ±0.0004	0.202 ±0.004	0.161 ±0.003
3 June	18	10	13.9 ± 0.30	0.182 ±0.006	47.5 ± 1.1	0.0145 ±0.0003	0.182 ±0.003	0.154 ±0.002
4 July	19	5	13.9 ± 0.26	0.195 ±0.005	49.9 ± 1.1	0.0138 ±0.0003	0.187 ±0.003	0.155 ±0.002
5 August	19	5	13.4 ± 0.25	0.209 ±0.007	57.7 ± 1.7	0.0140 ±0.0004	0.200 ±0.004	0.164 ±0.003
6 September	19	5	13.3 ± 0.40	0.228 ±0.008	56.1 ± 1.6	0.0142 ±0.0003	0.206 ±0.003	0.165 ±0.002
7 Oviparae September	18	10	13.8 ± 0.32	0.263 ±0.009		0.0143 ±0.0005	0.213 ±0.004	

Table 75: Growth and reproduction of apterous P.alni on A.cordata at 10°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult Weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R. G.R. $^{-1}$ mg mg^{-1} day^{-1}	rm
1 April	19	5	35.1 ± 1.3	0.286 ±0.012	20.6 ± 0.7	0.0154 ±0.0007	0.081 ±0.002	0.059 ±0.001
2 May	17	15	34.6 ± 1.3	0.274 ±0.009	21.3 ± 0.8	0.0148 ±0.0005	0.085 ±0.001	0.059 ±0.001
3 June	18	10	34.9 + 1.2	0.285 +0.009	24.4 + 0.9	0.0143 +0.0002	0.087 +0.0009	0.061 +0.0009
4 July	18	10	34.0 ± 1.2	0.246 ±0.008	19.3 ± 0.5	0.0134 ±0.0003	0.083 ±0.0008	0.058 ±0.001
5 August	17	15	35.0 ± 1.3	0.252 ±0.012	23.1 ± 0.6	0.0139 ±0.0005	0.082 ±0.001	0.058 ±0.0009
6 September	19	5	34.8 ± 1.4	0.251 ±0.013	24.8 ± 0.9	0.0142 ±0.0007	0.083 ±0.0009	0.061 ±0.001
7 Oviparae September	16	20	34.3 ± 1.3	0.289 ±0.018		0.0148 ±0.0006	0.089 ±0.002	

Table 76: Growth and reproduction of apterous P.alni on A.cordata at 15°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult Weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	19	5	20.4 ± 0.5	0.271 ±0.011	52.7 ± 1.0	0.0155 ±0.0006	0.143 ±0.004	0.124 ±0.0008
2 May	20	0	19.7 ± 0.6	0.253 ±0.009	50.4 ± 1.1	0.0147 ±0.0005	0.145 ±0.004	0.127 ±0.0010
3 June	20	0	19.0 ± 0.4	0.244 ±0.008	46.3 ± 0.8	0.0144 ±0.0004	0.149 ±0.005	0.127 ±0.0009
4 July	19	5	19.5 ± 0.4	0.240 ±0.009	40.1 ± 0.9	0.0142 ±0.0004	0.144 ±0.004	0.118 ±0.0008
5 August	18	10	20.2 ± 0.5	0.236 ±0.007	34.5 ± 0.8	0.0139 ±0.0003	0.141 ±0.003	0.119 ±0.011
6 September	19	5	19.3 ± 0.4	0.260 ±0.008	45.1 ± 0.9	0.0141 ±0.0002	0.148 ±0.004	0.120 ±0.0009
7 Oviparae September	20	0	19.8 ± 0.5	0.295 ±0.012		0.0145 ±0.0004	0.154 ±0.006	

Table 77: Growth and reproduction of apterous P.alni on A.cordata at 20°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult Weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	19	5	13.4 ± 0.31	0.246 ±0.009	44.9 ± 1.5	0.0157 ±0.0006	0.207 ±0.006	0.165 ±0.002
2 May	18	10	13.3 ± 0.32	0.240 ±0.008	40.4 ± 1.3	0.0146 ±0.0004	0.209 ±0.008	0.167 ±0.003
3 June	18	10	14.1 ± 0.41	0.196 ±0.005	36.5 ± 0.9	0.0140 ±0.0003	0.183 ±0.006	0.151 ±0.004
4 July	19	5	13.5 ± 0.31	0.145 ±0.006	22.7 ± 0.6	0.0135 ±0.0004	0.170 ±0.004	0.138 ±0.003
5 August	18	10	13.8 ± 0.39	0.163 ±0.007	30.3 ± 0.8	0.0139 ±0.0004	0.179 ±0.005	0.144 ±0.003
6 September	19	5	13.7 ± 0.33	0.205 ±0.008	37.2 ± 0.9	0.0142 ±0.0004	0.190 ±0.003	0.154 ±0.002
7 Oviparae September	17	15	13.8 ± 0.40	0.252 ±0.012		0.0144 ±0.0005	0.208 ±0.005	

Table 78: Growth and reproduction of apterous P.alni on A.incana at 10°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult Weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	18	10	35.3 ± 1.7	0.284 ±0.011	21.3 ± 0.8	0.0155 ±0.0004	0.082 ±0.0009	0.060 ±0.0008
2 May	18	10	34.2 ± 1.6	0.277 ±0.009	20.4 ± 0.9	0.0145 ±0.0005	0.084 ±0.001	0.061 ±0.001
3 June	17	15	34.9 ± 1.8	0.271 ±0.013	19.1 ± 0.8	0.0143 ±0.0003	0.083 ±0.0008	0.058 ±0.0008
4 July	18	10	35.4 ± 1.3	0.265 ±0.011	19.2 ± 0.7	0.0139 ±0.0004	0.083 ±0.0009	0.059 ±0.001
5 August	19	5	34.3 ± 1.5	0.277 ±0.014	21.4 ± 0.5	0.0144 ±0.0003	0.087 ±0.001	0.060 ±0.0009
6 September	16	20	34.8 ± 1.6	0.270 ±0.013	24.3 ± 0.6	0.0145 ±0.0004	0.084 ±0.0008	0.061 ±0.0008
7 Oviparae September	16	20	34.5 ± 1.5	0.293 ±0.011		0.0147 ±0.0005	0.088 ±0.0009	

Table 79: Growth and reproduction of apterous P.alni on A.incana at 15°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult Weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	19	5	19.8 ± 0.41	0.266 ±0.009	51.1 ± 1.2	0.0154 ±0.0006	0.144 ±0.005	0.129 ±0.0008
2 May	20	0	20.3 ± 0.40	0.235 ±0.009	40.3 ± 1.4	0.0143 ±0.0005	0.138 ±0.005	0.114 ±0.0012
3 June	18	10	19.1 ± 0.52	0.252 ±0.008	45.8 ± 0.9	0.0144 ±0.0003	0.145 ±0.003	0.124 ±0.0008
4 July	17	15	19.2 ± 0.52	0.230 ±0.008	40.0 ± 0.9	0.0134 ±0.0003	0.146 ±0.003	0.119 ±0.0008
5 August	19	5	20.4 ± 0.62	0.246 ±0.009	46.3 ± 1.2	0.0139 ±0.0004	0.139 ±0.003	0.118 ±0.0009
6 September	17	15	19.4 ± 0.34	0.262 ±0.011	49.8 ± 1.3	0.0144 ±0.0005	0.148 ±0.005	0.123 ±0.0011
7 Oviparae September	16	20	19.3 ± 0.32	0.290 ±0.014		0.0145 ±0.0006	0.156 ±0.007	

Table 80: Growth and reproduction of apterous P.alni on A.incana at 20°C

Generation (born)	Number reared	Nymphal mortality %	Development time/days	Adult Weight/mg	Fecundity (28 days)	Weight at birth/mg	M.R.G.R. mg mg^{-1} day^{-1}	rm
1 April	19	5	13.3 ± 0.40	0.236 ±0.009	45.8 ± 1.6	0.0151 ±0.0004	0.206 ±0.004	0.167 ±0.002
2 May	17	15	13.9 ± 0.32	0.245 ±0.013	50.3 ± 1.8	0.0145 ±0.0005	0.204 ±0.003	0.161 ±0.004
3 June	16	20	14.0 ± 0.33	0.199 ±0.008	39.1 ± 0.6	0.0141 ±0.0006	0.191 ±0.004	0.150 ±0.003
4 July	16	20	13.1 ± 0.32	0.178 ±0.004	35.4 ± 0.5	0.0135 ±0.0004	0.186 ±0.003	0.140 ±0.004
5 August	18	10	13.8 ± 0.40	0.220 ±0.008	36.1 ± 0.8	0.0141 ±0.0003	0.199 ±0.004	0.142 ±0.002
6 September	17	15	14.1 ± 0.44	0.234 ±0.009	45.6 ± 0.9	0.0143 ±0.0004	0.200 ±0.005	0.159 ±0.002
7 Oviparae September	18	10	13.9 ± 0.43	0.284 ±0.014		0.0146 ±0.0005	0.209 ±0.006	

weight decline in mid summer. For all aphids reared on A.glutinosa fecundity was greatest at 15°C being on average 58.62 nymphs per female, significantly greater than the 54.2 nymphs per female at 20°C ($d=13.58$, $p<0.001$), and considerably higher than the 25.0 nymphs produced at 10°C ($d=133.0$, $p<0.001$). Fecundity at 20°C was also very much higher than that at 10°C ($d=114.9$, $p<0.001$).

Aphids reared on A.cordata at the three temperatures (tables 75-77) showed similar seasonal trends to those observed in the field. There were no differences between generations in development time but aphids at 10°C took an average of 34.7 days to develop, significantly longer than the 19.7 days at 15°C ($d=29.50$, $p<0.001$), and the 13.7 days at 20°C ($d = 41.93$, $p<0.001$). The development time at 20°C was shorter than at 15 C ($d=33.12$, $p<0.001$). The weights of aphids reared showed a decline in midsummer and a rise again in autumn. Associated with this were falls in the fecundity and mean relative growth rate.

Aphids reared on A.incana (tables 78-80) again showed seasonal trends in weights, fecundity and growth rates, as observed in the field. Development times were similar for each generation at each temperature.

Within each generation there was no difference between the weights of aphids reared on A.glutinosa, A.cordata or A.incana at 10°C ($F6_{12}= 1.85$, $p>0.05$) or 15°C ($F6_{12} = 1.30$, $p>0.05$). However, at 20°C aphids of the fourth generation reared on A.cordata weighed 0.145mg, significantly smaller than those reared on A.glutinosa (0.195mg; $t=6.40$, d.f.=36, $p<0.001$), or A.incana (0.178mg; $t = 4.38$, d.f.=33, $p<0.001$). Fifth generation adults were also smaller on A.cordata than on A.glutinosa ($t=4.60$, d.f.=35, $p<0.001$) or A.incana ($t=5.36$, d.f.=34, $p<0.001$).

The intrinsic rate of increase was very similar on each alder for the

different temperatures. Regression analysis of the data indicated that there were strong relationships between the rm values on each alder and that the slopes of each line were not different from 1, nor the intercepts different from 0. At each temperature, P.alni thus achieves the same intrinsic rate of increase on A.glutinosa, A.cordata and A.incana (table 81).

To determine whether aphids change in weight once adult, individuals reared on A.glutinosa were weighed on the first, seventh and twenty-eighth day of adult life. The results of the change in weight over the first week of adult life are given in fig.168a,b,c. After the first week, small aphids at 15°C and 20°C gained weight, whreas large aphids lost weight. No change occurred when the teneral adult was 0.204mg at 20°C and 0.267mg at 15°C. If heavier than these figures aphids tended to lose weight and if lighter, to gain weight. This did not occur at 10°C (fig.168c The slope of the regression line was not significantly different from 1 ($t=0.44$, $p>0.05$) furthermore, the intercept was not different from 0 ($t=0.14$, $p>0.05$), indicating that no weight change occurred.

The form of the lines relating weight on day 1 to weight after 28 days were different to those reported above (fig.169a,b,c,). After 28 days, all aphids lost weight at 15°C and 20°C. However, at 10°C, there was still no significant change in weight ($t_{slope}= -0.29$, $p>0.05$, $t_{elev} = -0.26$, $p>0.05$).

At 15°C and 20°C on all three alder species there were significant relationships between the weight of an aphid and the number of offspring produced. Larger aphids were more fecund than small ones, over the 28 day period (table 82). At 10°C there was no relationship between weight and fecundity on any alder, but if the aphids were allowed to reproduce for a time period of development time plus prereproductive delay (used in calculating rm) the relationships became significant. This time period

Table 81: Regression equations for rm values on A.glutinosa, A.cordata and A.incana at 10°C, 15°C and 20°C

Treatment	Regression equation	Significance of: t= b from 1	a from 0	r
glutinosa v.cordata	y = 0.949x-0.000063	- 1.22 N.S.	0.02 N.S.	0.9851 ***
glutinosa v. incana	y = 0.941x+0.00064	- 1.41 N.S.	0.09 N.S.	0.9848 ***
cordata v. incana	y = 0.986x+0.0013	- 0.54 N.S.	0.12 N.S.	0.9946 ***

Note: *** :$p < 0.001$
N.S.:Not significant at $p \geqslant 0.05$

Figure 168:

The relationship between the weight of an apterous P.alni at adulthood and seven days later

(a) $20^{o}C$: $y = 0.677x + 0.066$

$r = 0.8786$, $d.f. = 62$, $p < 0.001$

(b) $15^{o}C$: $y = 0.738x + 0.070$

$r = 0.8151$, $d.f. = 51$, $p < 0.001$

(c) $10^{o}C$: $y = 1.051x + 0.010$

$r = 0.7689$, $d.f. = 58$, $p < 0.001$

- - - - -: $y = x$

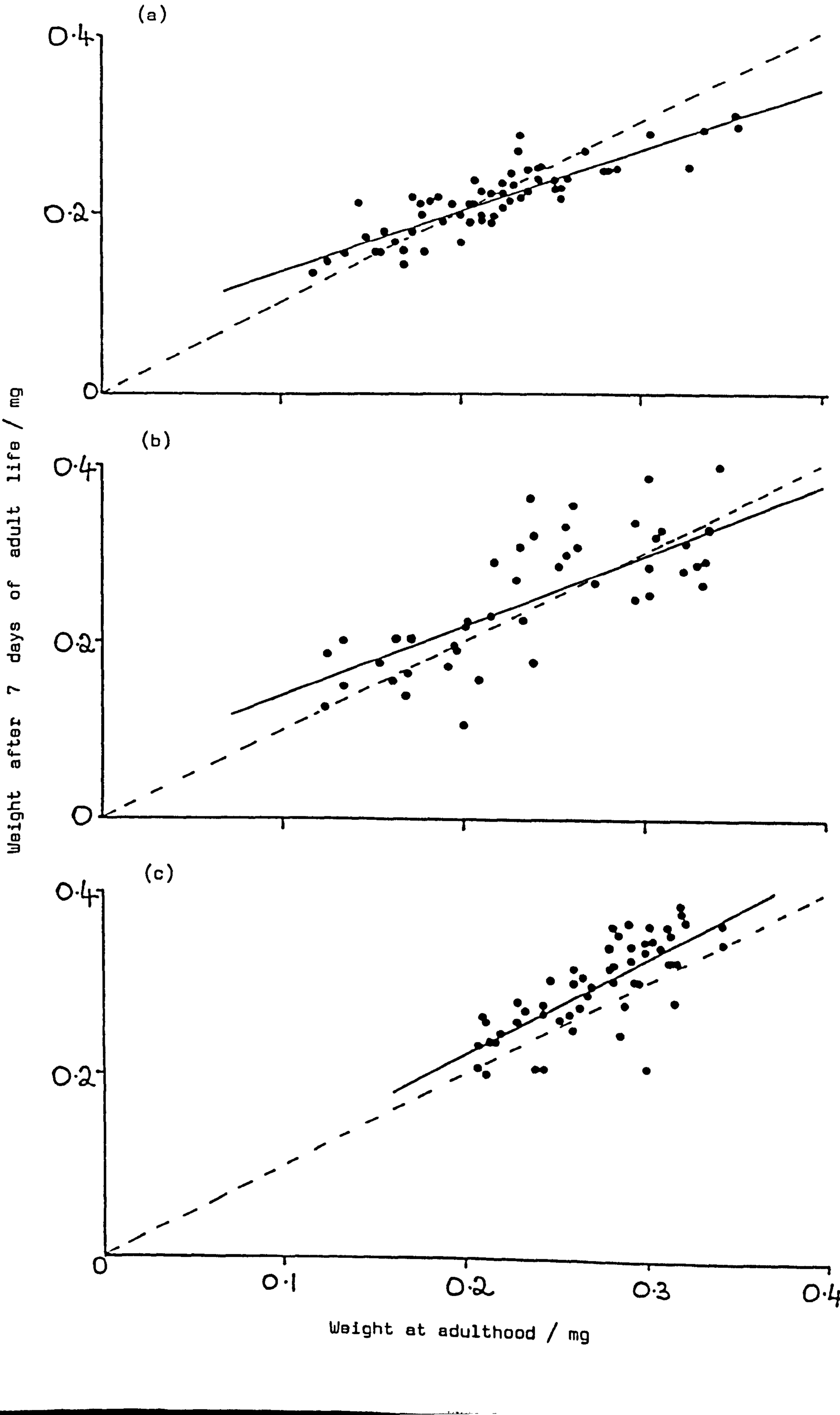

(a)
0·4
0·2
0
(b)
0·4
0·2
0
(c)
0·4
0·2
0
0·1
0·2
0·3
0·4
Weight after 7 days of adult life / mg
Weight at adulthood / mg

Figure 169:

The relationship between the weight of an apterous P.alni at adulthood and twenty-eight days later.

(a) $20^{o}C$: $y = 0.807x - 0.013$

$r = 0.9377$, d.f. = 60, $p < 0.001$

(b) $15^{o}C$: $y = 0.758x + 0.007$

$r = 0.9183$, d.f. = 50, $p < 0.001$

(c) $10^{o}C$: $y = 0.979x - 0.022$

$r = 0.8726$, d.f. = 56, $p < 0.001$

- - - -: $y = x$

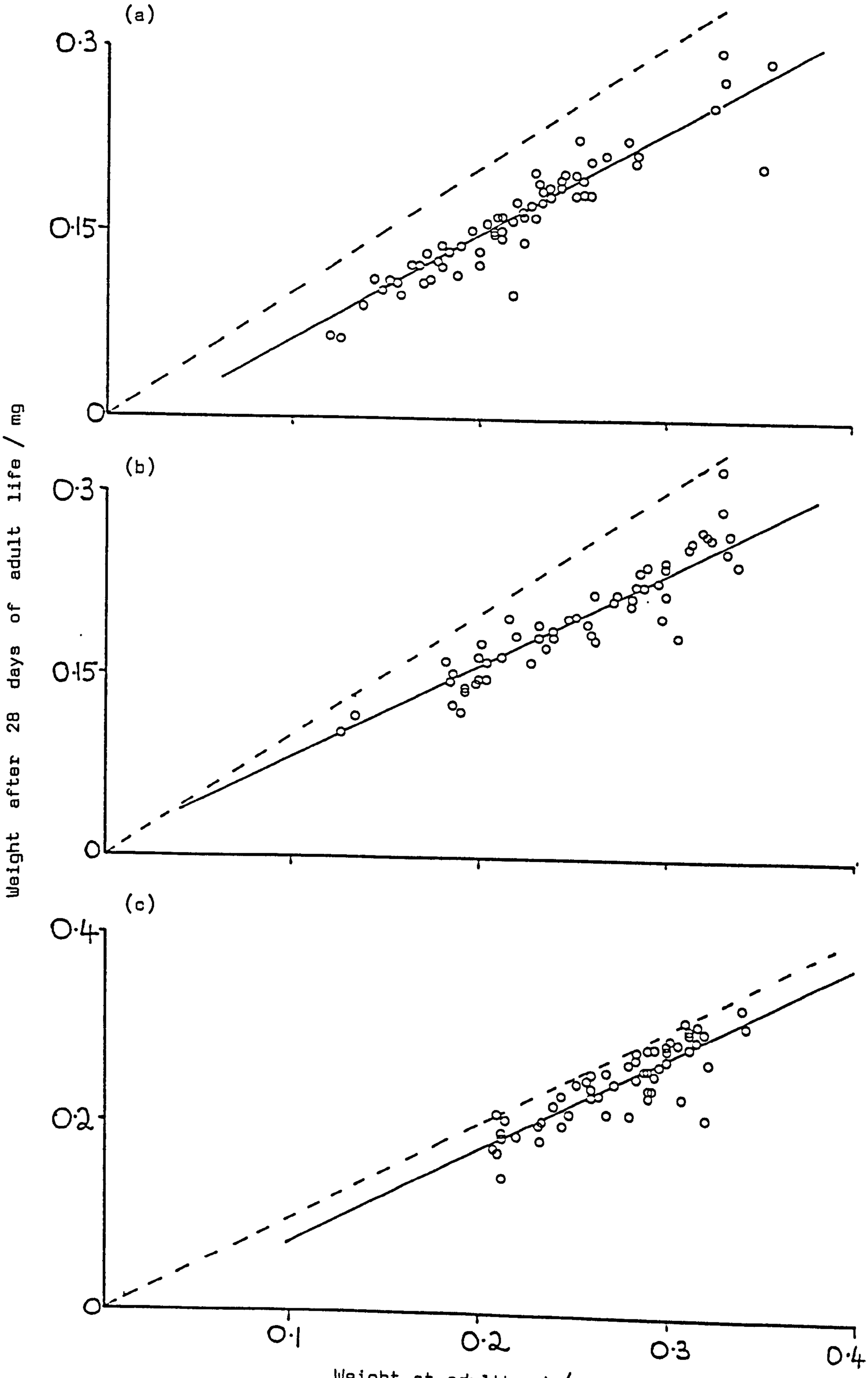

(a)
0·3
0·15
0
(b)
0·3
0·15
0
(c)
0·4
0·2
0
0·1
0·2
0·3
0·4
Weight after 28 days of adult life / mg
Weight at adulthood / mg

Table 82: The relationships between fecundity and adult weight of apterous P.alni on A.glutinosa, A.cordata and A.incana at 10°C, 15°C and 20°C.

Treatment	Regression equation	Significance of b from 0 t =	r	n
A.glutinosa 20°C	y = 140.3x + 24.5	11.08 ***	0.7084 ***	104
A.glutinosa 15°C	y = 87.7x + 35.9	7.44 ***	0.7030 ***	108
A.glutinosa 10°C	y = - 0.02x+ 25.1	0.74 N.S.	0.0974 N.S.	97
A.glutinosa 10°C (prereproductive time)	y = 134.9x + 8.9	13.14 ***	0.8668 ***	93
A.cordata 20°C	y = 152.1x + 4.5	8.33 ***	0.8398 ***	101
A.cordata 15°C	y = 104.1x + 19.0	8.62 ***	0.7101 ***	112
A.cordata 10°C	y = 0.06x+ 11.9	0.17 N.S.	0.0589 N.S.	102
A.cordata 10°C (prereproductive time)	y = 121.6x + 11.4	9.45 ***	0.8104 ***	98
A.incana 20°C	y = 103.7x + 14.6	8.87 ***	0.7769 ***	95
A.incana 15°C	y = 77.3x + 20.8	7.41 ***	0.7478 ***	99
A.incana 10°C	y = 0.03x+ 5.5	0.86 N.S.	0.090 N.S.	98
A.incana 10°C (prereproductive time)	y = 111.2x + 14.8	8.14 ***	0.7998 ***	90

Note: ***: $p < 0.001$ N.S.: not significant at $p \geq 0.05$

was 40 days long (table 82). Thus in 28 days there was no relationship between fecundity and weight, a possible result of the slower reproductive rate at this temperature. At higher temperatures aphids reproduced more quickly and realized most of their reproductive potential in 28 days. At 10°C this event did not occur after four weeks and even after the prereproductive period, the fecundity was less than that in 28 days for the higher temperatures.

The relationship between the mean relative growth rates and intrinsic rates of increase are summarized in table 83. There was a good relationship between the two quantities at each temperature and on each alder species with b, the slope of the line, being significantly greater than zero in all cases. However, only at 10°C was b not significantly different from 1, indicating that at this temperature MRGR and rm were very similar. At 15°C and 20°C b was significantly less than 1 indicating that the value of MRGR tended to be larger than that of rm, a likely result of the shorter development time in the denominator of the growth rate equation. At 10°C , development time was 2.5 times that at 20°C and 1.8 times that at 15°C. The longer development time caused MRGR to be smaller and closer to rm. The shorter development time at 20°C and 15°C meant that the prereproductive period was shorter and therefore relatively fewer offspring were produced, causing rm to be small, relative to MRGR. At 10°C the converse was true and the two values were closer.

A graph of the development rate (the reciprocal of development time) and temperature is given in fig.170. Each point is the mean value for all aphids reared at the particular temperature. Extrapolating the regression line to the point where development rate is theoretically zero produced a threshold temperature for P.alni of 3.56°C.

Table 83: The relationships between mean relative growth rate (x) and intrinsic rate of increase (y) of P.alni

Treatment	Regression equation	Significance of b from 0 t=	Significance of b from 1 t=	r	n
A.glutinosa 10°C	y = 0.88x - 0.01	13.02 ***	1.76 N.S.	0.8632 ***	93
A.glutinosa 15°C	y = 0.27x + 0.09	6.56 ***	17.76 ***	0.6529 ***	110
A.glutinosa 20°C	y = 0.47x + 0.07	10.06 ***	11.54 ***	0.6733 ***	109
A.cordata 10°C	y = 0.87x + 0.01	10.55 ***	0.21 N.S.	0.8496 ***	98
A.cordata 15°C	y = 0.45x + 0.05	6.87 ***	8.52 ***	0.8318 ***	114
A.cordata 20°C	y = 0.61x + 0.04	7.19 ***	4.66 ***	0.8006 ***	107
A.incana 10°C	y = 0.88x + 0.05	12.15 ***	0.22 N.S.	0.8044 ***	90
A.incana 15°C	y = 0.57x + 0.03	6.86 ***	5.12 ***	0.8510 ***	103
A.incana 20°C	y = 0.49x + 0.06	4.67 ***	4.68 ***	0.6478 ***	101

Note: *** $p < 0.001$ N.S. not significant at $p \geq 0.05$

Figure 170:

Temperature and development rate of <u>P.alni</u>

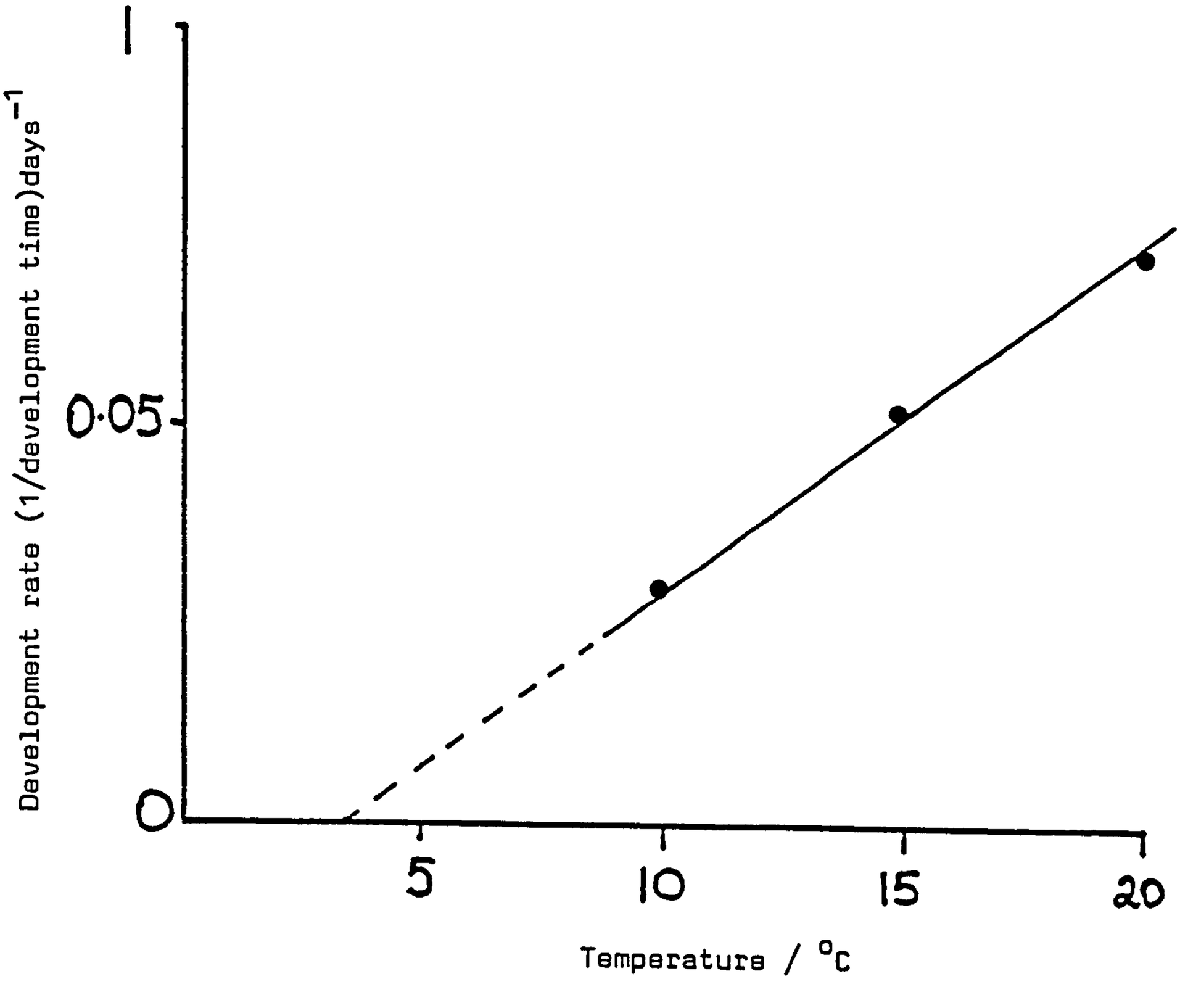
Temperature at which D.R. is theoretically zero: $3.56^{o}C$

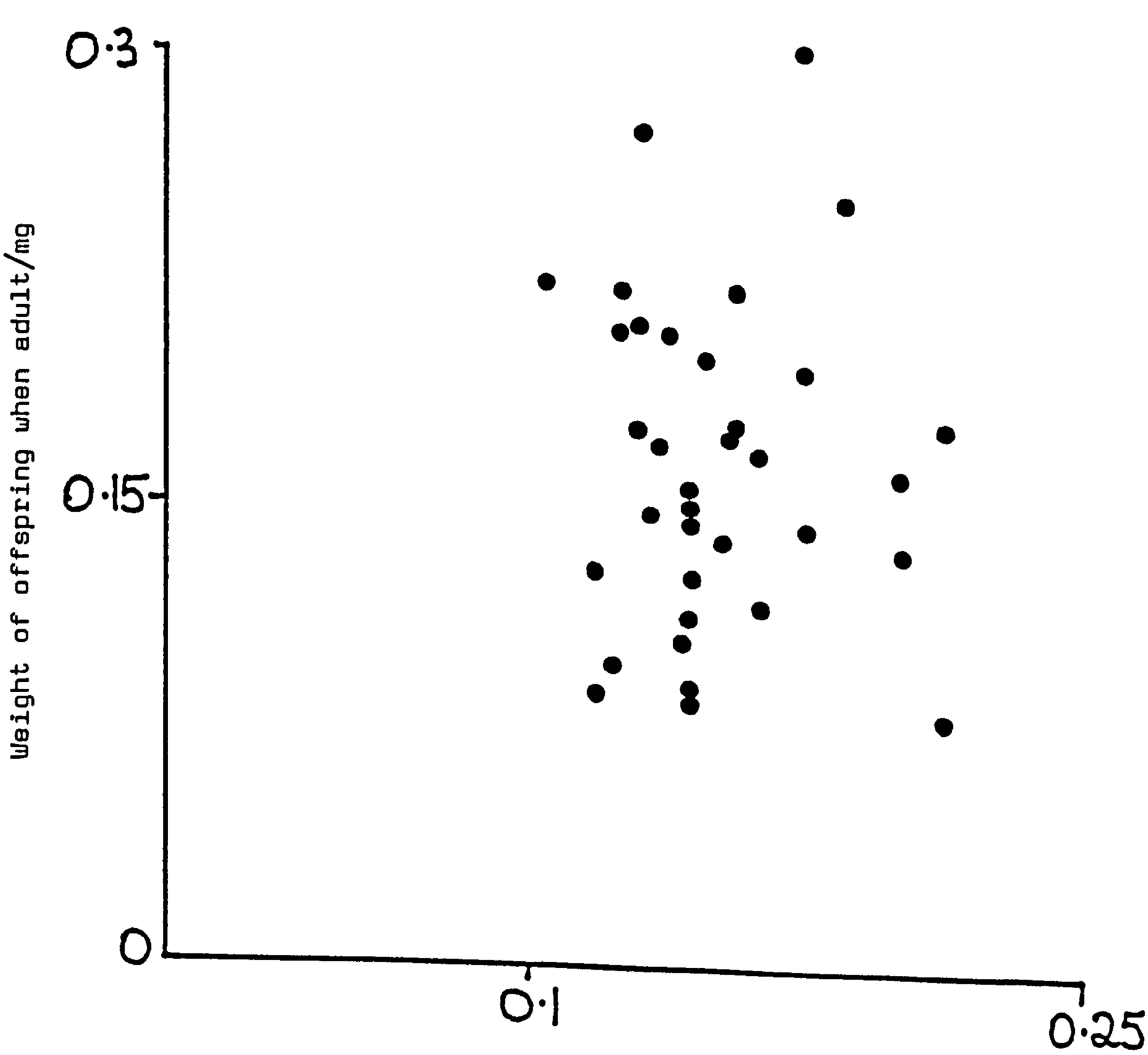
Figure 171:

The weight of a mother and the weight of her offspring when adult

$y = -0.078x + 0.176$

$r = -0.039$, d.f. = 33, $p > 0.05$


Development rate (1/development time)days^{-1}
0·05
0
5
10
15
20
Temperature / °C


Weight of offspring when adult/mg
0·3
0·15
0
0·1
0·25
Weight of mother / mg

To examine the relationship between the teneral weight of a mother and that of her offspring, aphids were reared to maturity and weighed. Single offspring were reared on the same sapling as the mother had been and their teneral adult weight recorded. The experiment was conducted at 20°C on A.glutinosa. The results are presented in fig.171. There was no relationship between the teneral weight of the mother and the weight of her offspring when adult. The slope of the regression line was not significantly different from zero ($t=0.22, d.f.=33, p>0.05$).

A batch of apterous aphids of the second generation were reared on windbreak LF125 (A.glutinosa). All were born on the same day and were weighed at the teneral adult stage, before reproduction had begun. Immediately after weighing they were dissected and the total number of embryos and those with pigmented eyes recorded. There was a strong relationship between the weight of the aphid and the total number of embryos it contained (fig.172a). Larger aphids contained more embryos than small aphids. Larger aphids also contained more advanced embryos, with pigmented eyes, than did small individuals (fig.172b). If the number of advanced embryos is expressed as a proportion of the total content, then large aphids contain a higher proportion of advanced embryos than do small individuals (fig.172c).

Aphids of the second generation were reared on A.glutinosa at 10°C, 15°C and 20°C singly and in groups. The weights of aphids at maturity were recorded to determine the effect of crowding on adult weight. Isolated aphids at 20°C weighed on average 0.207mg, significantly larger than those which were crowded, which weighed 0.163mg ($t=5.63, d.f=40, p<0.001$). Isolated individuals at 15°C were considerably larger (0.269mg) than crowded aphids (0.199mg) ($t=4.11, d.f.=46, p<0.001$). Crowding aphids at 10°C also resulted in smaller individuals weighing 0.247mg compared to 0.289mg for isolated specimens ($t=2.21, d.f.=44, p<0.05$).

Figure 172:

Weight of apterous adults and embryo content

(a) The relationship between adult weight and total embryo content in P.alni

$y = 76.4x + 5.2$

$r = 0.916$, d.f. = 40, $p < 0.001$

(b) The relationship between adult weight and the number of advanced embryos (with pigmented eyes) within

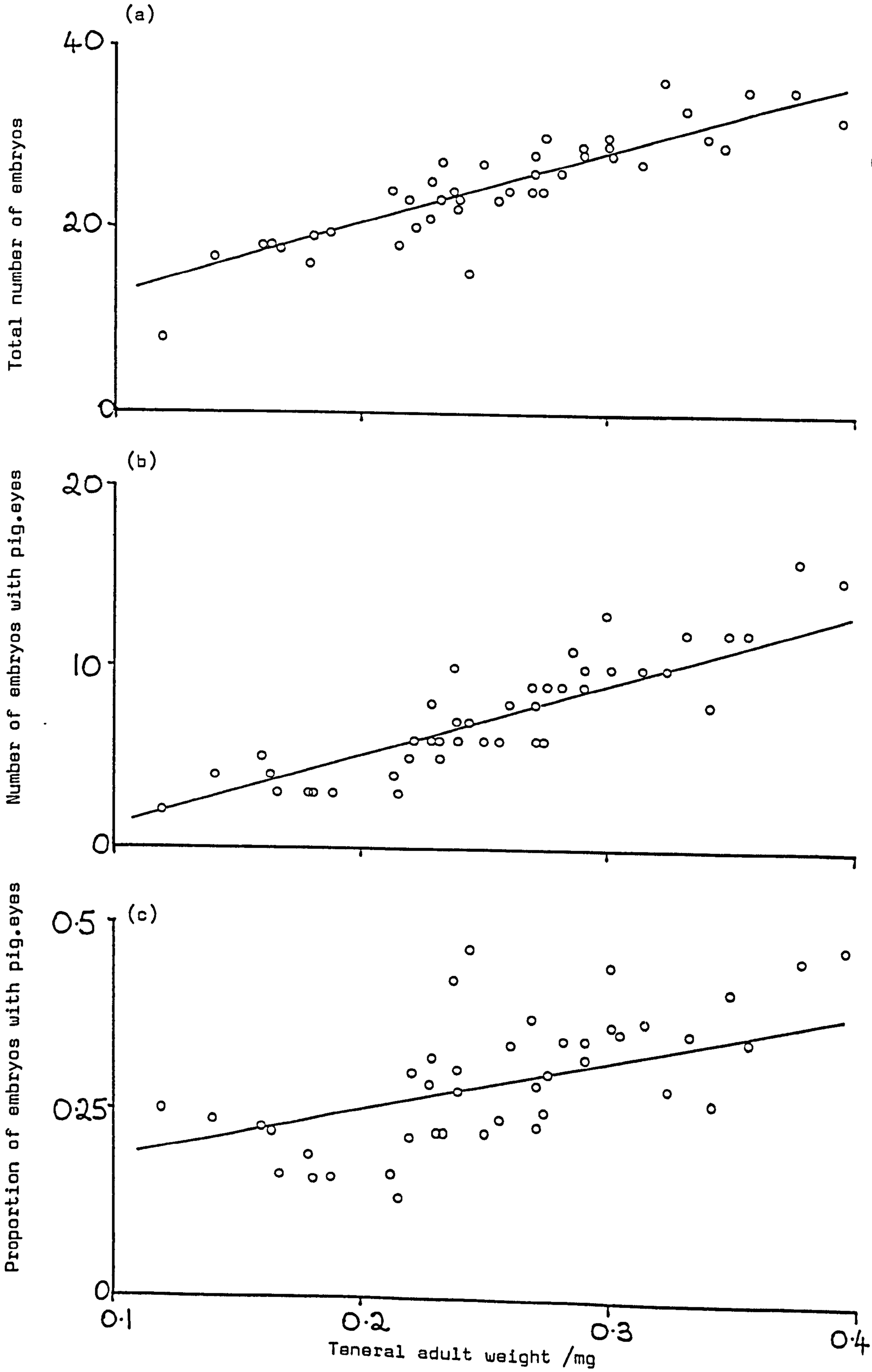
$y = 40.9x - 3.1$

$r = 0.899$, d.f. = 40, $p < 0.001$

(c) The relationship between adult weight and the proportion of embryos having pigmented eyes

$y = 0.66x + 0.18$

$r = 0.609$, d.f. = 40, $p < 0.001$


(a)
40
20
0
Total number of embryos
(b)
20
10
0
Number of embryos with pig.eyes
(c)
0·5
0·25
0
Proportion of embryos with pig.eyes
0·1
0·2
0·3
0·4
Teneral adult weight /mg

Random samples of adult aphids were taken from the field during the period of abundance. The weights of the aphids collected at East Malling from LF125 and WM110 are shown in figs.173-176. Weights of apterae declined during the summer, rising again in September. The embryo content also followed a similar seasonal trend. Alatae when present also showed a decline in weight and embryo content as summer progressed. Those aphids present after the period of peak population abundance were therefore of poor quality, being small and with a low productive potential. The graphs of aphid weight in figs173-176 are similar to those reared in cages depicted in fig.167a,b. All aphids whether crowded in natural populations or reared singly in cages showed similar seasonal declines in weight.

Aphids of each successive generation reared in the field were dissected at maturity and the number of ovarioles counted. The fundatrix generation contained 8, as did all other generations, including the oviparae. Ovarioles were contained in two ovaries, with four ovarioles in each. No variation was found within generations in over 200 aphids dissected.

5.2.4. Discussion

Fluctuations in numbers of D.platanoidis on sycamore within and between years depends to a great extent on the nutritive quality of the host plant (Dixon, 1970b). When the nutritive quality of the leaves is poor, a density-dependent reduction in reproductive rate occurs, which can lead to cessation of reproduction at high densities (Dixon,1966). Poor food quality results in smaller aphids in summer than in spring or autumn (Dixon,1970b;1971b;Lorriman 1980). The decline in food quality is illustrated by examining trends in soluble nitrogen content of leaf tissue.

Figure 173:

Seasonal change in weight and advanced embryo content of field collected P.alni adults from LF 125, 1982

(a) Weight of apterae

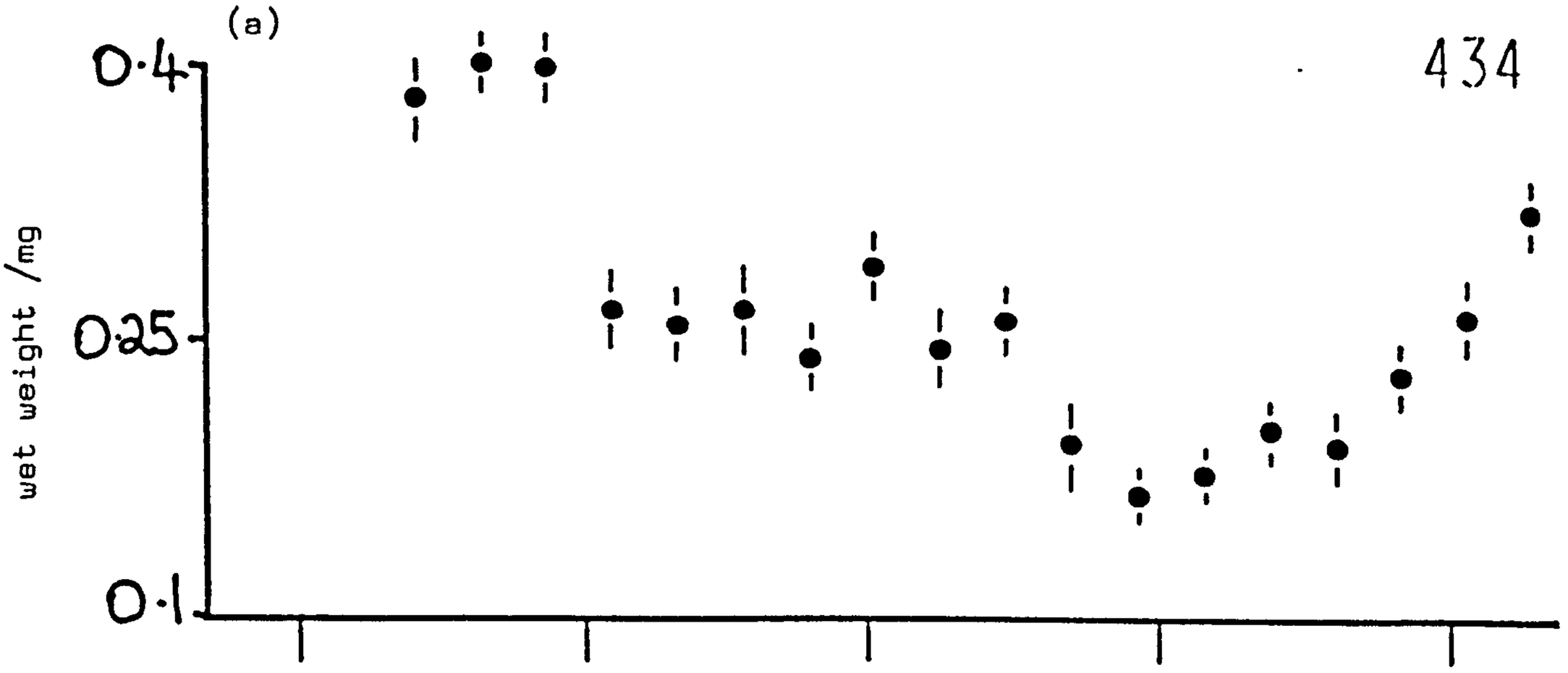
(b) Embryo content of apterae

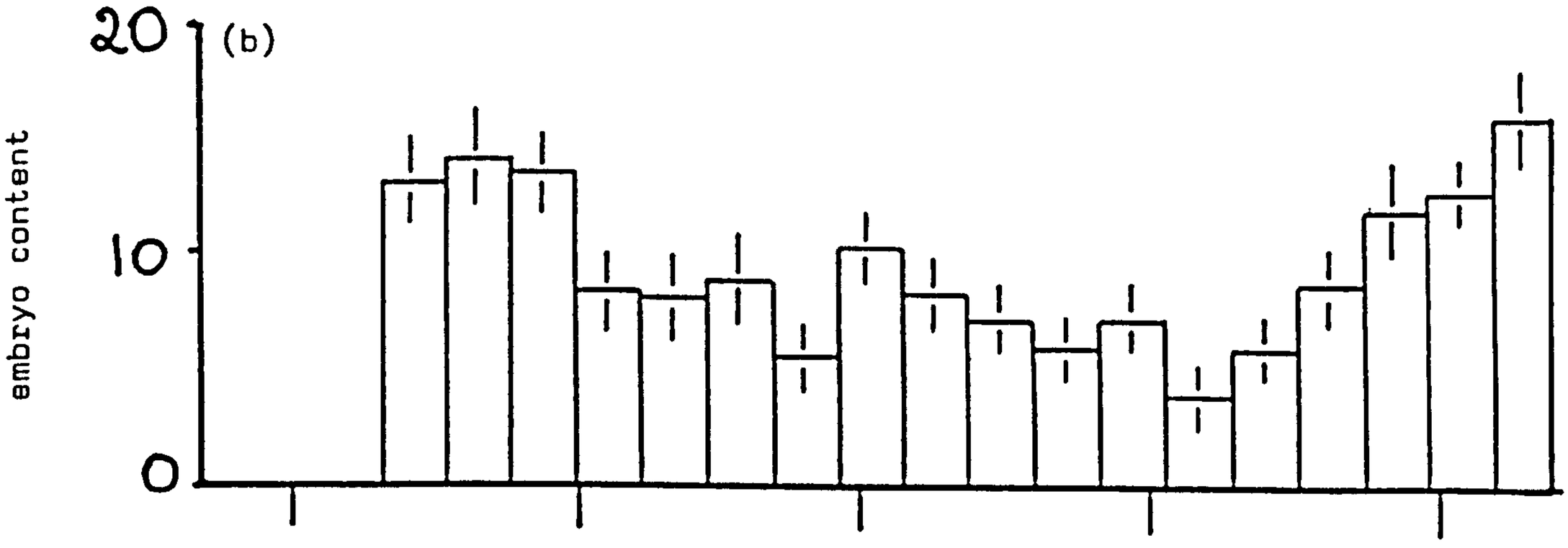
(c) Weight of alatae

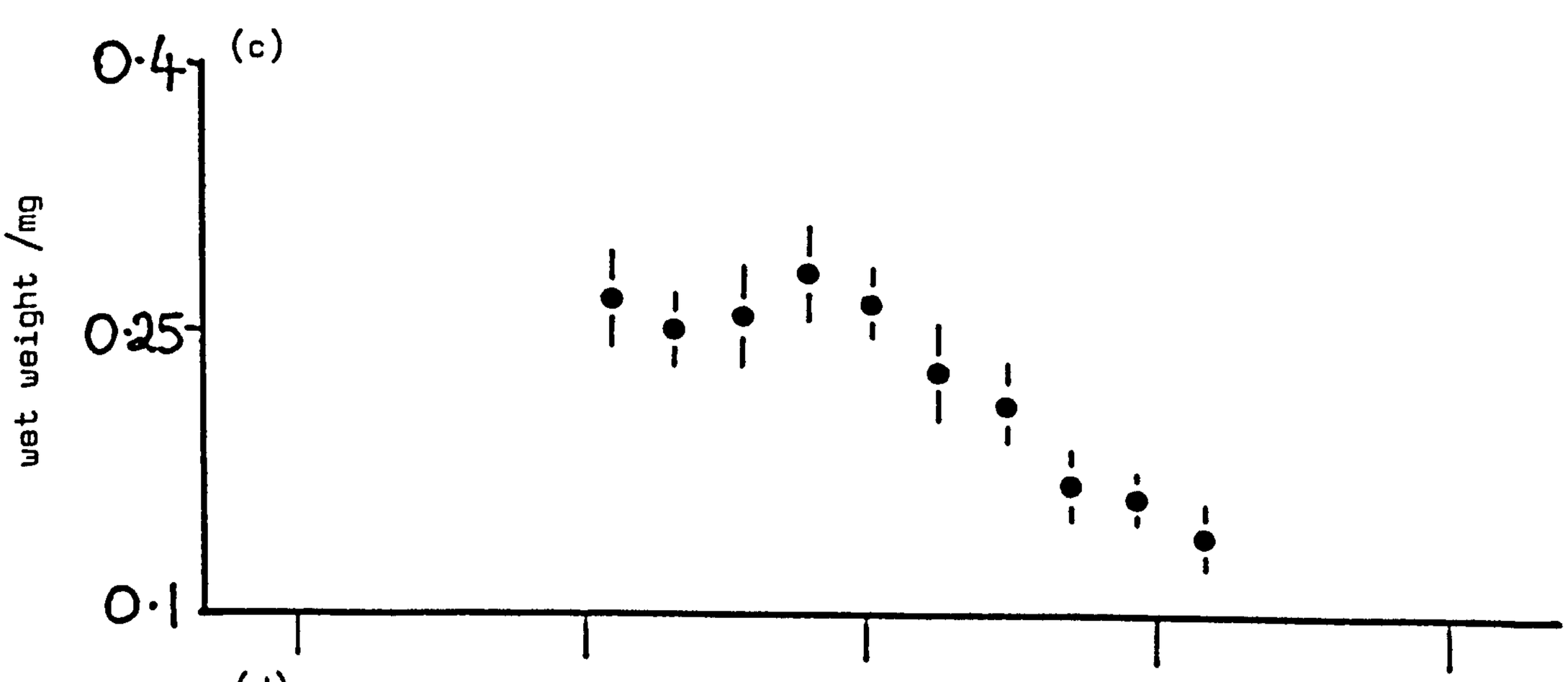
(d) Embryo content of alatae

Values given are means with 95% confidence limits

(a)


0·4
0·25
0·1
wet weight /mg


20
10
0
embryo content
(b)


0·4
0·25
0·1
wet weight /mg
(c)

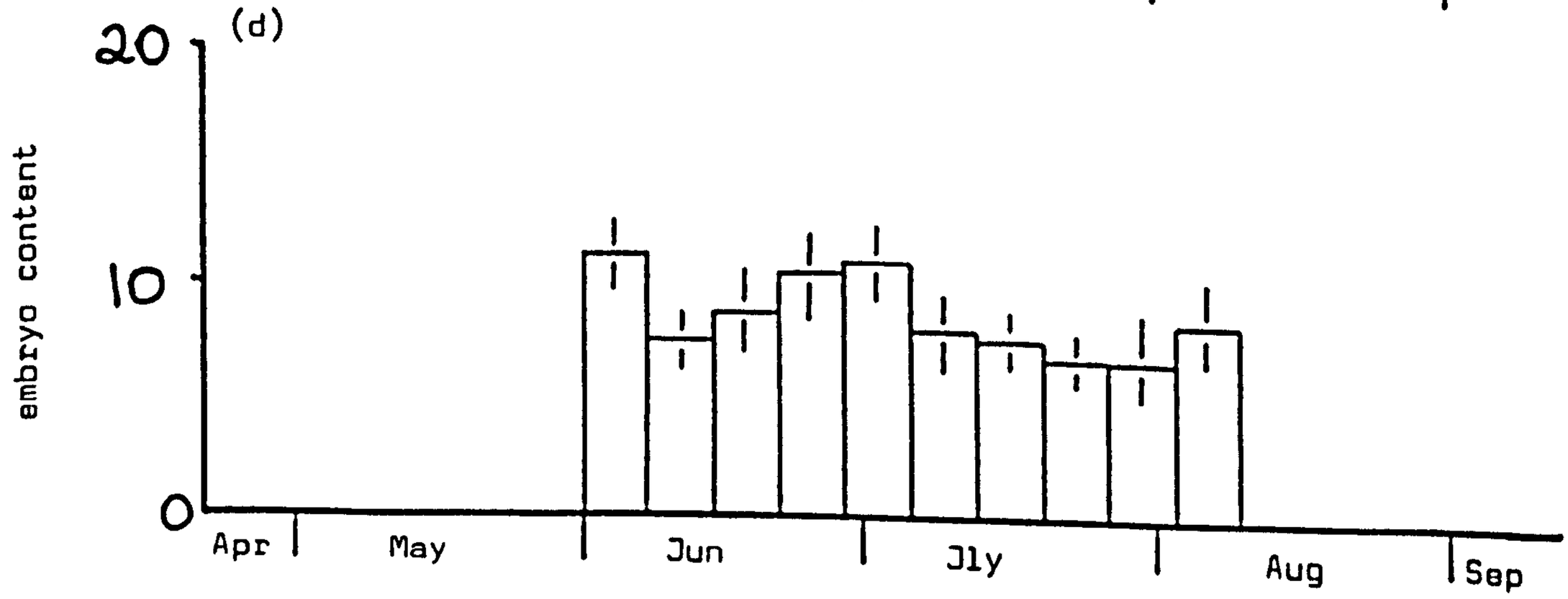

20
10
0
embryo content
(d)
Apr
May
Jun
Jly
Aug
Sep

Figure 174:

Seasonal change in weight and advanced embryo content of field collected P.alni adults from WM 110, 1982

(a) Weight of apterae

(b) Embryo content of apterae

(c) Weight of alatae

(d) Embryo content of alatae

Values given are means with 95% confidence limits

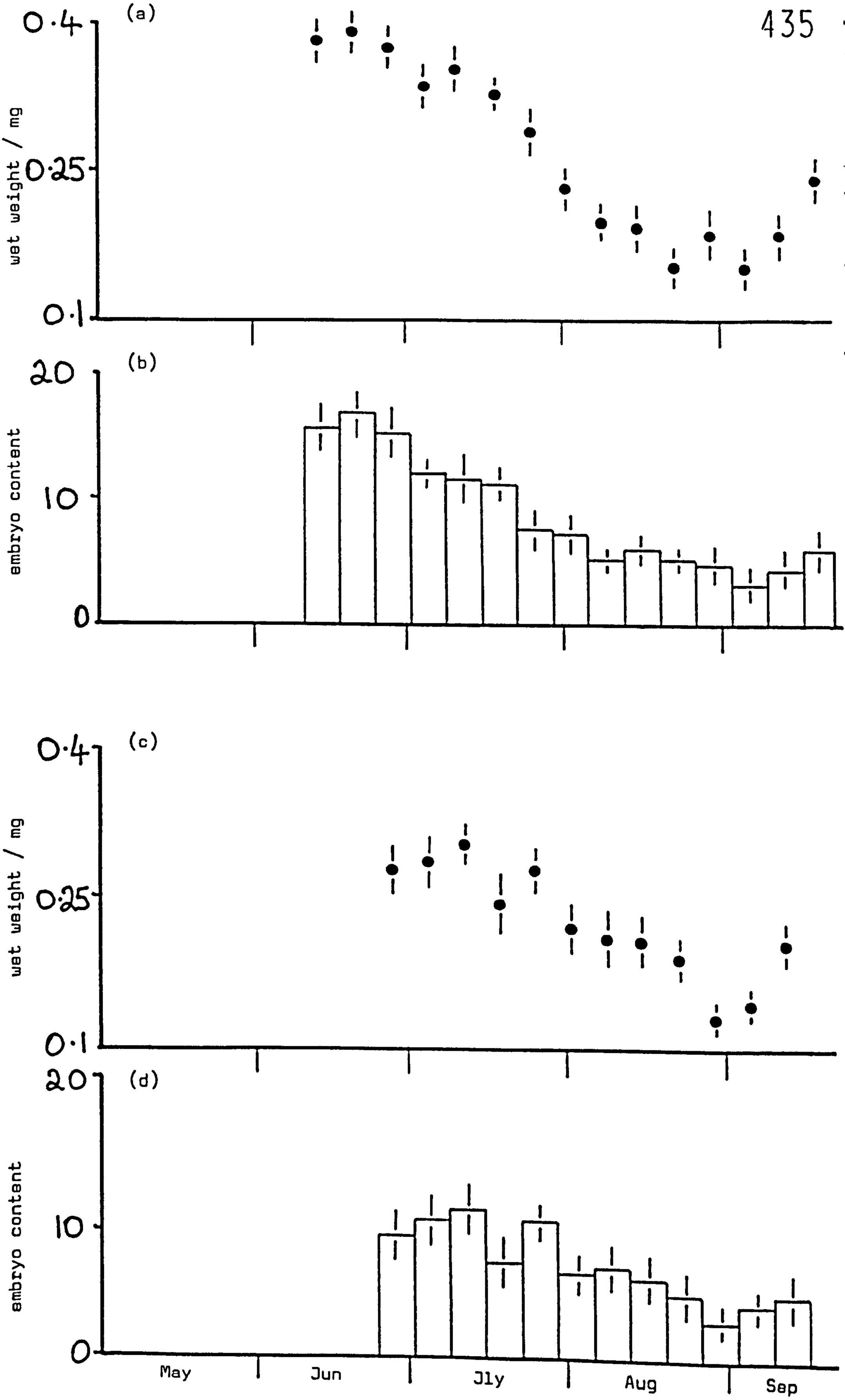

(a)
0·4
0·25
0·1
wet weight / mg
(b)
20
10
0
embryo content
(c)
0·4
0·25
0·1
wet weight / mg
(d)
20
10
0
embryo content
May
Jun
Jly
Aug
Sep

Figure 175:

Seasonal change in weight and advanced embryo content of field collected P.alni adults from LF125, 1983.

(a) Weight of apterae

(b) Embryo content of apterae

(c) Weight of alatae

(d) Embryo content of alatae

Values given are means with 95% confidence limits

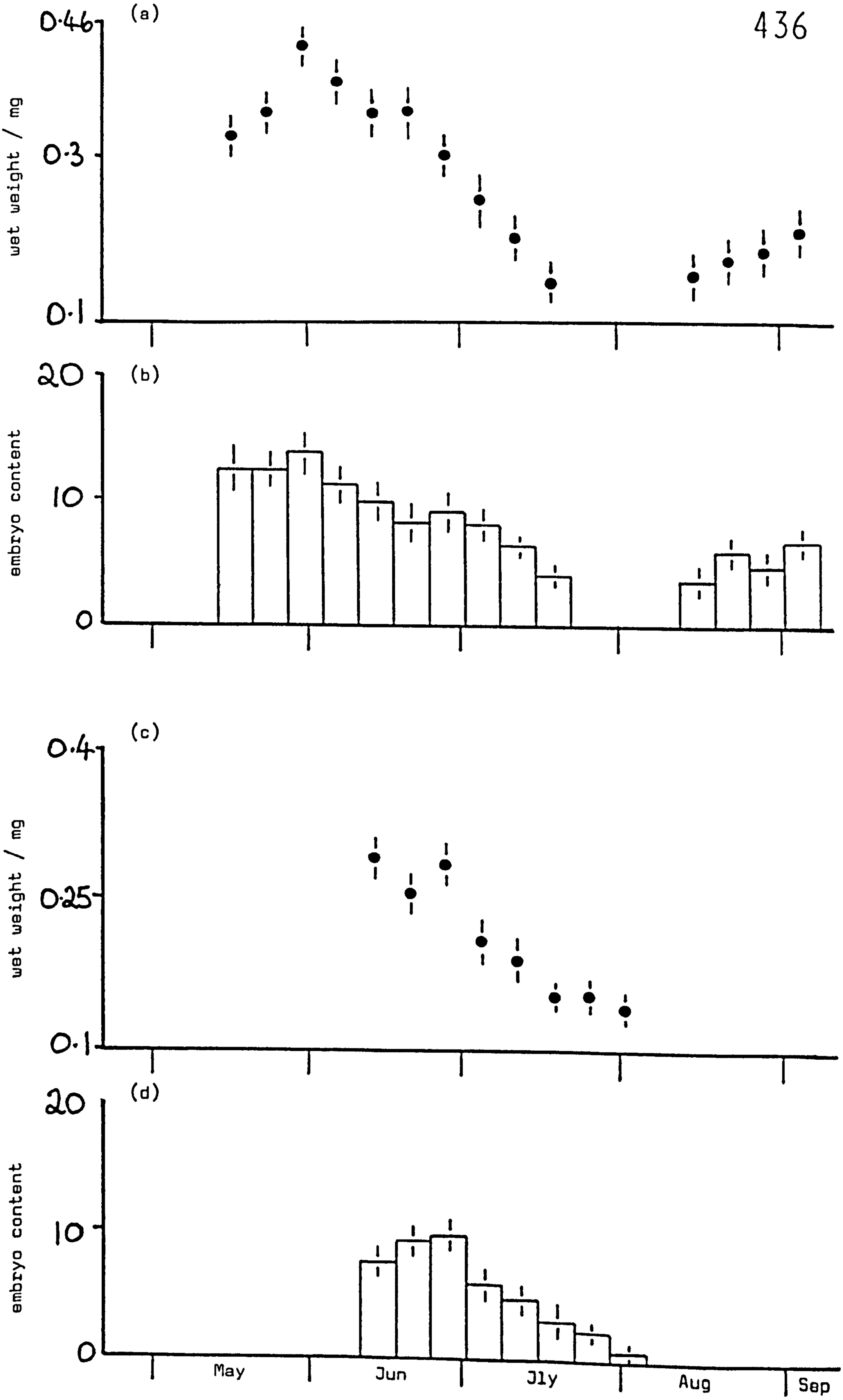

(a)
0·46
0·3
0·1
wet weight / mg
(b)
20
10
0
embryo content
(c)
0·4
0·25
0·1
wet weight / mg
(d)
20
10
0
embryo content
May
Jun
Jly
Aug
Sep

Figure 176:

Seasonal change in weight and advanced embryo content of field collected P.alni adults from WM 110, 1983

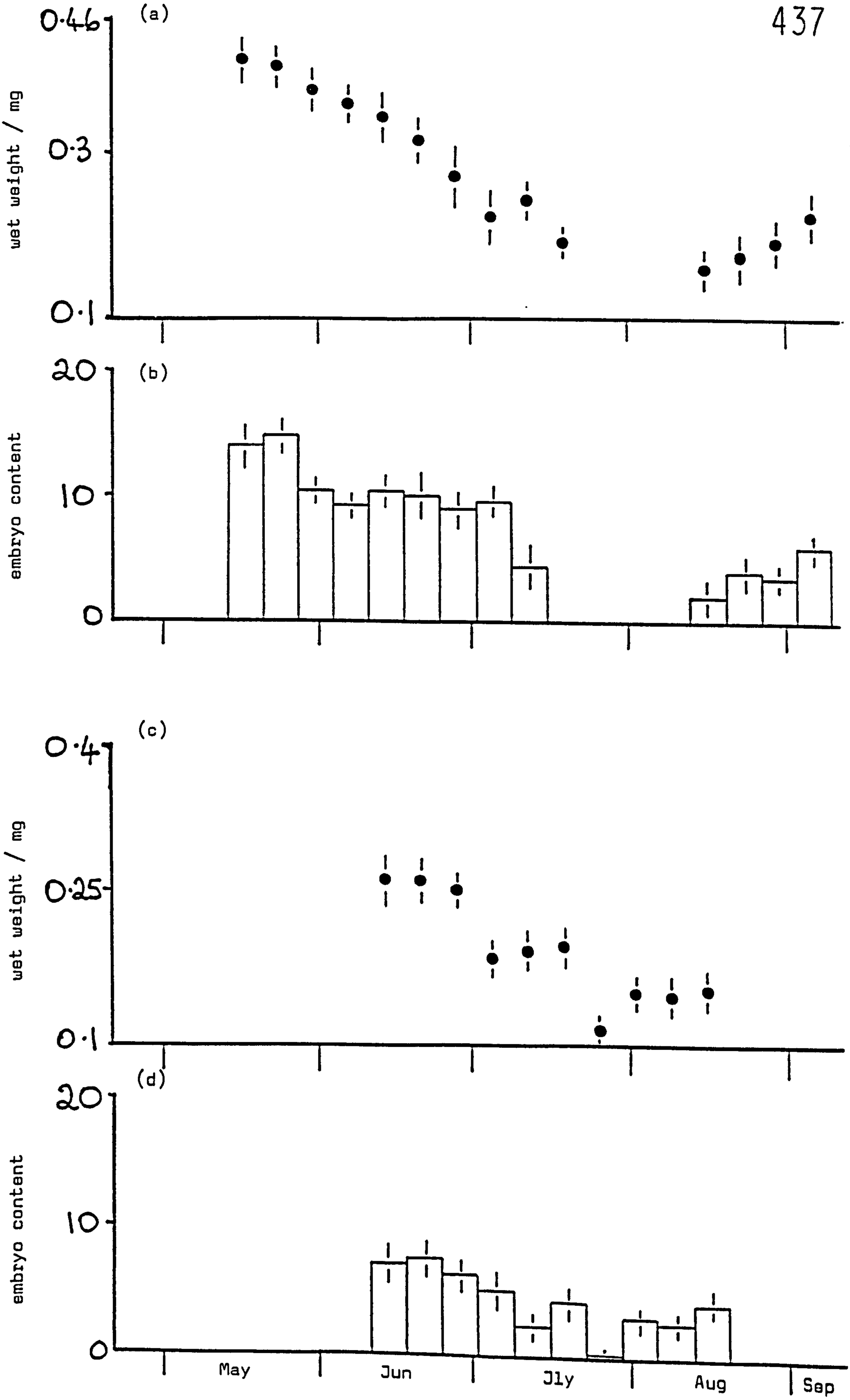
(a) Weight of apterae

(b) Embryo content of apterae

(c) Weight of alatae

(d) Embryo content of alatae

Values given are means with 95% confidence limits


(a)
0·46
0·3
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wet weight / mg
(b)
20
10
0
embryo content
(c)
0·4
0·25
0·1
wet weight / mg
(d)
20
10
0
embryo content
May
Jun
Jly
Aug
Sep

P.alni also exhibits a seasonal decline in weight and fecundity. The decline follows a similar pattern to that reported for soluble nitrogen content of alder leaves. Even when temperature is kept constant, seasonal trends still occur, due to the changing food quality. When alder trees were maintained from before bud burst in a constant environment of 20°C and 16hr light no such seasonal trend was noticed in the aphids reared upon them. It therefore appears that the saplings were providing a constant food supply, due to the lack of the normal changing environmental cues of temperature, daylength and water stress to which plants may normally respond.

In field situations a complex array of factors may interact to determine aphid size. Crowding of individuals has been shown to reduce aphid size in A.pisum (Murdie,1969a) and D.platanoidis (Dixon,1970b). Crowding of apterae of P.alni significantly reduced the size attained by the adults. Such size reduction may be due to mutual interaction between aphids. When individuals of D.platanoidis are crowded, dense aggregations are not formed due to the restlessness of individuals, caused by kicking movements when approached by another aphid (Dixon,1963). Such activity results in more time wandering about and less time feeding. However, as aphids reared from birth in isolation also show a seasonal decline in weight, crowding is not the only factor determining size in P.alni.

It is likely that the poorer food quality provided by the alder in summer relative to that available in spring and summer has an effect. Individuals of D.platanoidis are smaller on leaves of poor quality (Dixon 1970,b). The trend in weight of P.alni when temperature and crowding are controlled mirrored closely that of food quality, measured in field conditions.

High temperatures have been shown to exert a considerable influence on aphid growth. Increasing temperature generally results in a decrease in

size (Murdie, 1969a) and an increase in fecundity (Dean, 1974). For many species, development time is shortened at temperatures up to 20°C but any subsequent temperature increase has little effect. Development time in P.alni appeared to be a constant at any given temperature, despite changes in food quality. The optimal temperature for fecundity was 15°C. Accepting that this could be due to the differences between trees used for the experiments, this compares well with the 15°C reported for M.viciae (Milne,1971) and 12°C for M.evansi (Perrin, 1974). Developmental threshold temperatures vary according to climate (Campbell et al, 1974). Thresholds are higher in warm summer climates. That calculated for P.alni is 3.56°C, similar to the 4.3°C reported for M.persicae (Sharaf Eldin,1970), 4.5°C for A.pisum and 5.6°C for M.viciae (Milne,1971). M.evansi has a reported threshold of -3.4°C (Perrin, 1974) and its ability to overwinter as a viviparous adult is attributed to this. An aphid in a warm climate such as C.juglandicola in Southern California has a high threshold of 9.7°C (Nowierski et al, 1983). Using the threshold temperature and the developmental time observed at each temperature the thermal constants for P.alni were 225.2 day degrees at 20°C, 225.4 day degrees at 15°C and 223.5 day degrees at 10°C. Temperatures in the field were obviously not constant and fluctuations in these may have affected aphid development. Siddiqui, Barlow and Randolph (1973) reported that alternating temperatures in a low range (5-20°C) caused swifter development of A.pisum whereas temperatures above this caused increased development time. Possibly at 25-30°C heat stress occurred, temporarily arresting development. Such stress was also proposed for M.evansi at 25°C (Perrin,1974) and it is likely that P.alni would experience similar stress. The fact that fecundity was reduced at 20°C suggests that this may be approaching stressful temperatures for this aphid. Daylength has been shown to interact with temperature and light intensity to affect size in aphids (Wyatt and Brown,1977). It is possible therefore that changing conditions in the field may have affected growth.

Reproductive potential is a preprogrammed feature of aphid life cycles (Wellings et al,1980). P.alni has 8 ovarioles in all generations. In this it differs from other studied members of the Callaphididae in which the fundatrices contain two more ovarioles than the subsequent generations. In Drepanosiphum acerinum (Walker), E.tiliae and E.punctipennis fundatrices possess ten ovarioles. Those of D.platanoidis possess twelve (Wellings et al, 1980). This fact may explain why fundatrices reared on the windbreaks were little more fecund than adults of the second generation. Differences may therefore have been due to the better food quality available earlier in the year. The fact that P.alni does not appear to anticipate seasonal changes in food quality such as is implied by the changing ovariole number of other Callaphididae (Wellings et al,1980) may be in response to the relatively good food supply provided by alder throughout the year. On a host such as this which fixes nitrogen, the aphid is able to reproduce throughout the summer and little advantage may be gained in summer by having fewer ovarioles. Ward, Wellings and Dixon (1983) found that on nutritionally poor hosts, aphids with more ovarioles were less likely to survive than those with few. This may be of little consequence to P.alni and the advantages of having more ovarioles such as increased fecundity (Ward,Dixon and Wellings 1983) would outweigh the disadvantages of survival problems. It would be interesting to investigate ovariole numbers in aphids on other nitrogen-fixing plants.

All summer generations possess 8 ovarioles, therefore reproductive investment in each generation is similar, size differences being caused by differences in embryo content. Small aphids at maturity contain fewer embryos than large individuals and a smaller proportion of these are in an advanced state. Small aphids mature more embryos after becoming adult resulting in an increase in weight in the first week of adult life, whereas large aphids lose weight in this time. Therefore

when food quality begins to improve in late summer and crowding conditions are much less severe, individuals of P.alni are able to reproduce quickly and take advantage of the improved conditions. As no variability in ovariole number occurs, it is unlikely that prereproductive mortality occurs as a result of reproductive investment (Ward, Wellings and Dixon, 1983) and that all individuals will have increased fecundity when the nutritive status of the host improves (Ward, Dixon and Wellings,1983). Such an increase in reproduction was noted in field populations when relatively large numbers of aphids remaining after early pruning resulted in high autumnal populations (chapter 2). When pruning occurred late, no noticeable increase took place due to aphid numbers being so low.

Murdie (1969b) considered that the possession of an adult pre-reproductive maturation period was the most important single factor enabling recovery of A.pisum from crowd-induced size decrease. As this period in P.alni varies from 1.3 days at 20°C to 4.1 days at 10°C it is likely that this is another factor enabling P.alni to recover its size in late summer generations. It is noticeable that size recovery attains a greater degree and is earlier on A.glutinosa than on A.cordata or A.incana, another reflection on the changes in food quality provided by these hosts in late summer.

The lowest weight and fecundity of aphids reared in the field occurred after the date of peak population density in 1983 and 1984. Such an occurrence is likely to be responsible for the delay in recovery of populations noticed after previous declines. Only when the aphids become more fecund with increased size in late summer did populations begin to recover. Therefore as summer advances, increasing temperatures, worsening food quality and increased crowding cause successive generations of aphids to be smaller and less fecund. The total recruitment to the

population begins to level off and the populations decline when mortality (migratory flight due to crowding) exceeds recruitment. A similar situation was proposed to explain the dynamics of T.tuberculatus populations (Lorrimer,1980) although Lorriman and Llewellyn (unpublished) consider that food quality plays little part in growth and reproduction and that loss of recruitment is caused by increasing temperature.

The alatae of P.alni when produced in response to crowding exhibit different reproductive strategies to their apterous counterparts. In contrast to apterae they mature with few embryos within them and none with pigmented eyes. A detailed comparison of the ovarian development of apterous and alate A.craccivora was reported by Elliott and McDonald (1976). Development reflected the production of nymphs by apterae almost immediately after adult moult whereas alatae did not reproduce for 1-2 days. The prereproductive period of alatae is longer than that for apterae in P.alni and embryo maturation appears to occur after flight or after 3-4 days if flight has not occurred in this time. There is no evidence to suggest that feeding of P.alni influences the quality of its food, thus migratory flight appears to be in response to conditions of current adversity, that is competition for food and space. There is no need for alatae to attain reproductive parity with apterae in the first few days of adult life as happens with A.fabae (Dixon and Wratten,1971). An alata which flies is likely to encounter alder which is in a similar physiological condition to that which it left, but conditions of crowding may be less severe. So long as the total progeny is as near as possible to the apterous morph, then the colonization of new alder hosts may be successfully achieved. A similar situation was reported for alatae of S.avenae and M.dirhodum (Wratten,1977). As alatae of P.alni contain 8 ovarioles their lesser fecundity compared to apterae may be a result of the maintenance of wing musculature competing with the reproductive system for the available amino-nitrogen. Alatae retain the ability to fly throughout adult life

unlike some aphids such as A.fabae (Johnson,1953). Tree dwelling aphids tend not to autolyse their wing muscles (Dixon,1973) and this may be related to their relatively long life in which they may experience a range of favourable and unfavourable conditions.

Colonization of A.incana and A.cordata appears to be generally unsuccessful in the field. Only in autumn 1982 were oviparae produced on A.cordata. Nymphs were found the following spring but no population increase occurred, a result of the lack of suitable feeding sites due to bud burst being so much later than aphid hatch in this species. No oviparae were ever found on A.incana. The question remains therefore as to why aphids may be reared to maturity on these two species in field and laboratory. The answer may lie in the external physiology of the leaf. Under the scanning electron microscope the surface of A.glutinosa is ridged with veins and with few small hairs (plate 4,a). That of A.cordata is very smooth, the veins hardly emanating from the leaf surface (plate 4,b). The surface of A.incana is extremely hairy (plate 4,c) and the downy appearance of the leaves may be how it obtained its name of 'white alder'. The leaf surface of A.glutinosa is more amenable to young nymphs, where ridges may provide shelter from wind. Wind is a major mortality factor in D.platanoidis numbers (Chambers,1979) and it was noticeable that when sampling took place on days of high wind or heavy rain aphids were clustered close to the veins. On calm days they were distributed over the leaf surface, in a manner remarkably similar to that described for D.platanoidis by Dixon and McKay (1970). On leaves of A.cordata there was nowhere to hide when leaves were brushed against each other by wind. The mass of a leaf relative to that of an alder aphid is of the order of 10,000 to one; thus any aphid being struck by a leaf is likely to be dislodged. On A.incana the physical barrier of the mass of pubescence may prevent first instar nymphs from settling down to feed resulting in death by starvation or dislodging. A similar occurrence

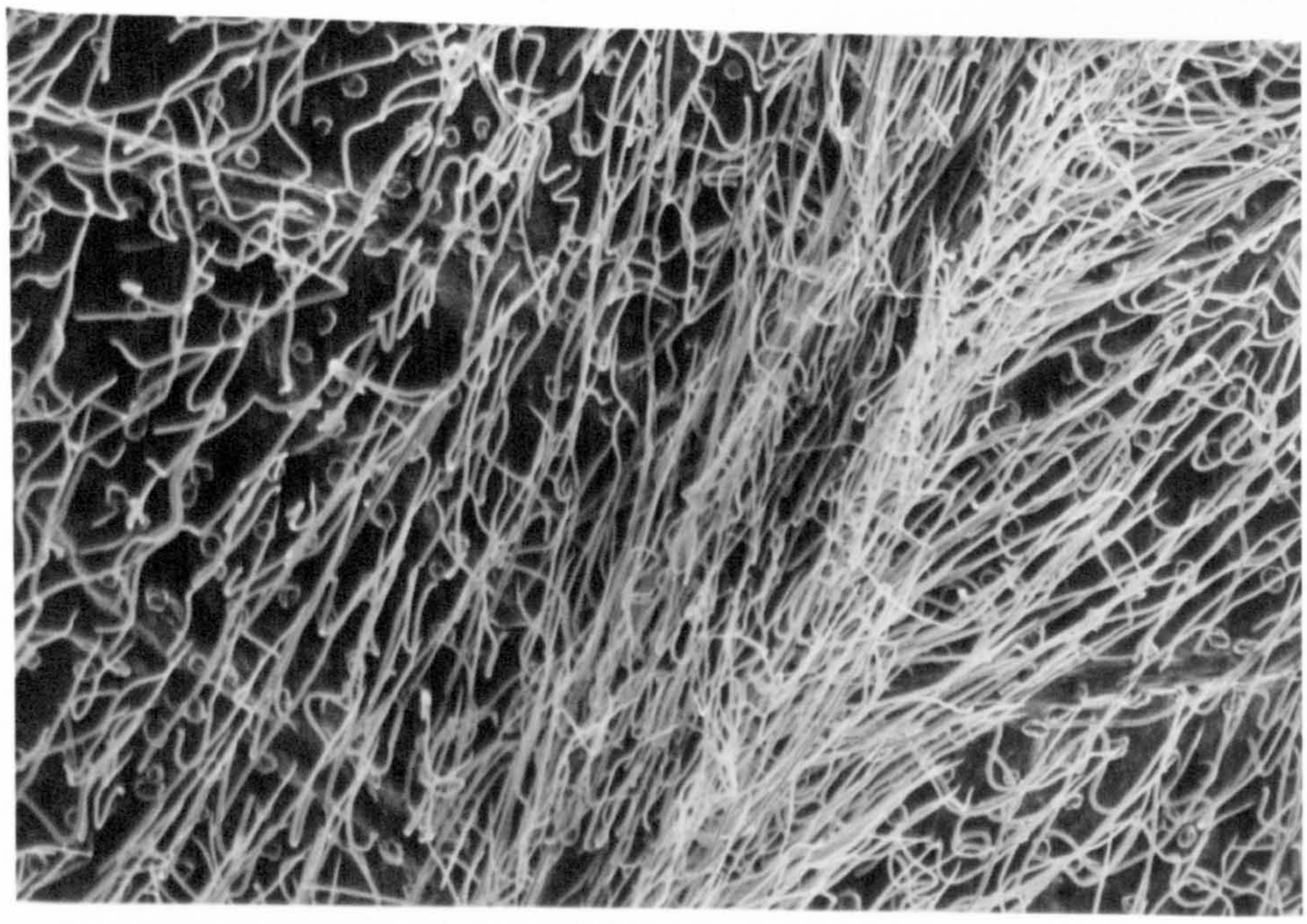
PLATE 4

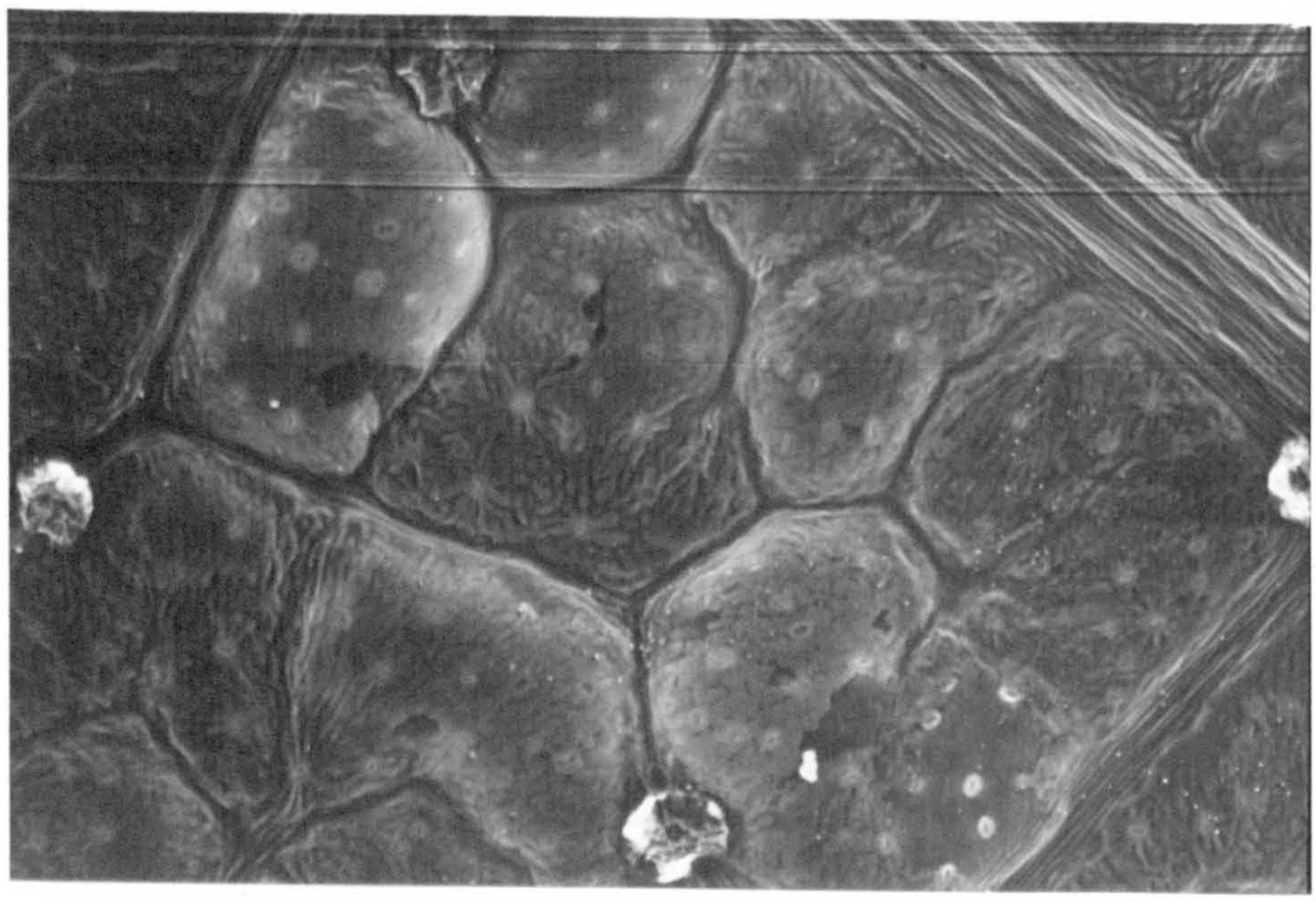
Leaf surfaces of alder species

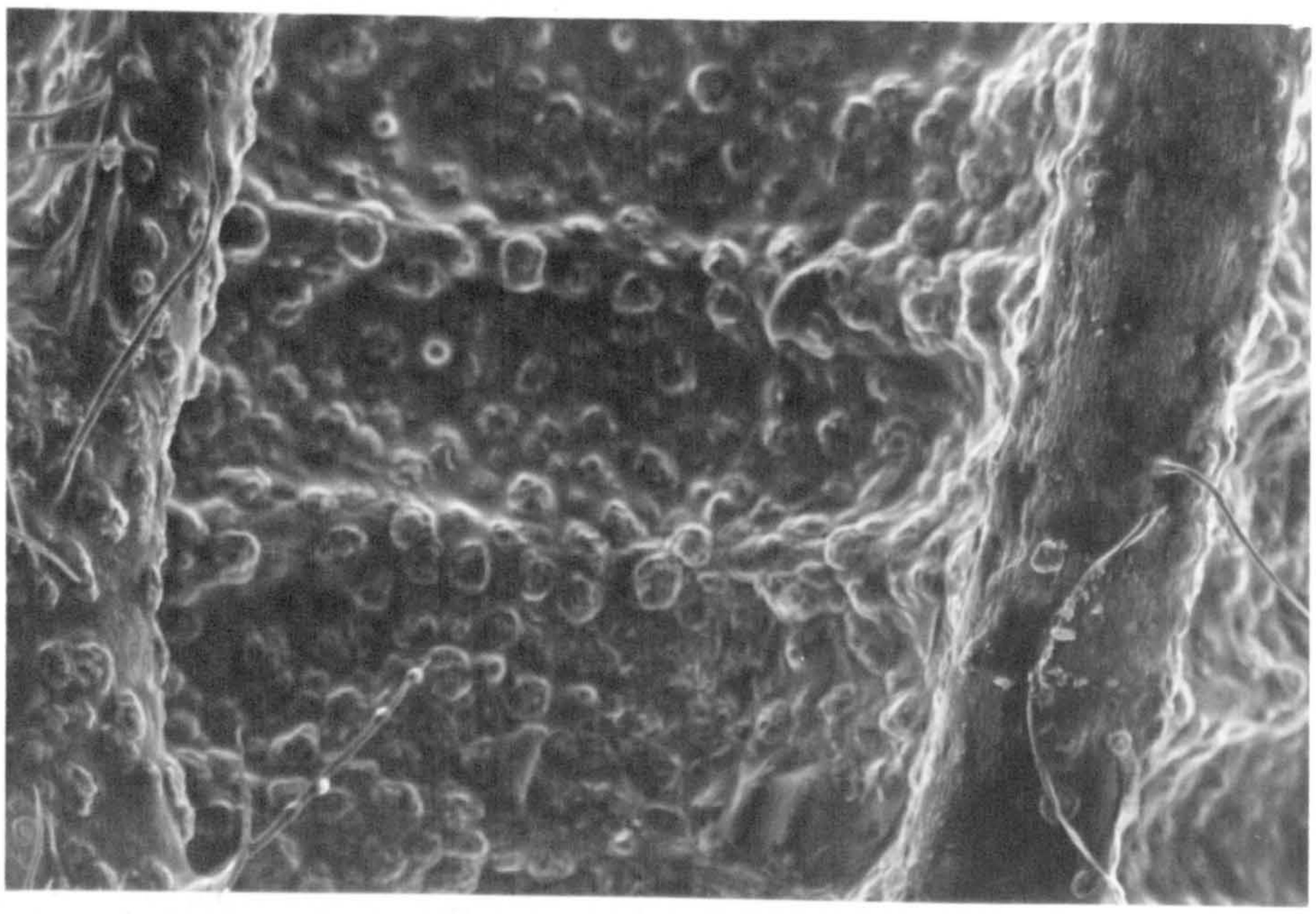
(a) A.glutinosa X 45

(b) A.cordata X 45

(c) A.incana X 45







was reported by Carter (1982) involving the leaf surface of various Tilia species and their susceptibility to attack by E.tiliae. In that study limes with pubescent leaves were shown to be'resistant' to young nymphs, these dying through starvation. When the pubescence was removed aphids could be reared successfully. Many other examples of pubescence on leaves conferring resistance to aphids have been reported. An example is that of Roberts and Foster (1983) who found that R.padi populations were considerably less on pubescent-leaved wheat. In the growth room where wind or rainfall do not exist, aphids are able to feed on A.cordata and A.incana leaves without fear of dislodging. Mortality thus appears to be considerably less in these constant environments. The fact that caging aphids in the field obviously confers upon them the advantage of shelter may lend support to the proposal of Dixon (1977) that caging confers advantages upon aphids. However as large numbers died even when in cages it seems likely that the advantages are not great.

The fact that different results may be obtained in controlled conditions and in the field emphasizes the need for comparable experiments in all studies of 'plant resistance'.

Throughout this study, variation in performance of individuals on different trees has been noted. Trees provide a very variable food supply and great differences may exist between them (Dixon,1970b). Genotypic differences in both plant and aphid may occur to cause these differences. The performance of Uroleucon rudbeckiae (Fitch) on Rudbeckia laciniata has been shown to depend upon the genetical composition of both aphid and host (Service,1984a) and differences in field performance of Uroleucon caligatum (Richards) on Solidago spp has also been shown to be the result of genetical variation (Moran, 1981). McVean (1953) noted that a physiological variability was likely to exist between stands of A.glutinosa especially as external morphology was extremely variable. It is therefore likely that differences between trees are the result of genetical

variation modified by environmental conditions. Genetical variation may occur in populations of P.alni but the rearing of large numbers on one windbreak appeared to even out any such differences and produce reasonably consistent results.

Population dynamics of P.alni therefore appear to be influenced by crowding, host plant physiology and temperature. Increased crowding, poor food quality and higher temperatures result in successively smaller, less fecund aphids. When migratory flight occurs the population collapses when mortality exceeds recruitment. When numbers are relatively high in late summer following the collapse or by pruning, populations increase again in autumn due to the increased fecundity and size of aphids. The improved quality of these aphids is due to the cooler temperatures less crowded conditions and improved food supply in autumn. Nitrogen fixation by alders causes nitrogen levels in the leaf tissue to be relatively high to that reported for many other trees. The advantages to P.alni are that food quality is never poor for long and reproduction may continue throughout the summer.

Leather and Dixon (1984) found a very close relationship between the intrinsic rate of increase and the mean relative growth rate for R.padi over a range of host plants, temperatures and generations. Dixon (1985a) also found that a similar relationship existed for a range of aphids. In this study a good relationship for P.alni existed over the range of temperatures used but only at $10^{o}C$ was the slope of the line not different from 1. This was a consequence of the relatively shorter development time at $15^{o}C$ and $20^{o}C$. Thus only at $10^{o}C$ does an increase in MRGR result in a corresponding increase in rm.

The interactions of the aphid with predators and how populations of these may be affected by changes in aphid numbers are reported in the next chapter.

Chapter 6. INTERACTION BETWEEN P.ALNI AND B.ANGULATUS IN FIELD AND LABORATORY

6.1. LABORATORY FEEDING EXPERIMENTS

6.1.1. Introduction

B.angulatus, the black-kneed capsid is a predatory mirid found on a range of British trees including alder (Southwood and Leston, 1959). Collyer (1952) studied its biology on apple where it has been shown to be an important predator of the fruit tree red spider mite, P.ulmi (Collyer 1953) and eggs of the codling moth, Cydia pomonella (Glen 1977a) On lime (T. x europaea) it has been shown to feed on E.tiliae and the leafhopper Alnetoidea alneti (Dahlbom) (Glen, 1975). The food requirements of the bug preying on E.tiliae have been studied by Glen (1973).

Possible prey in addition to P.alni are the alder psyllid Psylla alni L. and the ciccadellids Kybos smaragdula Fallen, Typhlocyba jucunda Herrich-Schaeffer and A.alneti. Adult Psylla alni are robust, active insects several times larger than P.alni. The nymphs of this psyllid are protected by a large secretion of wax threads. Since B.angulatus hatches from the egg in late June/early July when Psylla alni are almost completely adult it is unlikely that this is the main prey species. The leafhopper species are also active adult forms when B.angulatus appears. In the present study leafhoppers were only found in any numbers on LF125. They appeared to be virtually absent from WM110 and did not occur on A.cordata or A.incana. Skinner (1983) using beating samples of A.glutinosa found cicadellidae to be much less common than Psylla alni or P.alni. It is therefore highly likely that the aphid P.alni forms the main food supply for B.angulatus on alder. The food requirements of the bug preying on this aphid were therefore examined in the laboratory.

6.1.2. Materials and Methods

Capsid nymphs were reared in clip-cages similar to that described by Noble (1958), (dimensions 2cm x 1cm high). Each cage was clipped on to a fresh A.glutinosa leaf. A.cordata was not used as B.angulatus and P.alni are rarely found upon it; neither was A.incana as leaf hairs may impede searching and capture by young instars of the bug (Glen,1975). Aphids were placed upon the leaves and the bug introduced into the cage using a fine camel hair brush, moistened with water. Leaves and aphids were renewed every other day. Cages were placed in plastic boxes with moist tissue paper lining the base. The humidity in the boxes was 90-95% measured by cobalt thiocyanate paper (Solomon, 1945). The boxes were placed in a constant temperature of $15^{o}C \pm 1.3^{o}C$ and 16 hours daylength.

Eggs were obtained by caging a number of wild collected adults the previous autumn on A.glutinosa saplings, infested with aphids. Muslin cages enclosed the saplings and these were left in place throughout winter in the University of London's Botanical Garden, Egham, Surrey. According to Muir (1966a) the mean date of first egg hatch is the end of the first week in June, calculated from forty years' temperature data. In early June the muslin was removed and all the young wood cut into convenient lengths and placed in plastic boxes after the leaves were removed. The boxes were lined with moist tissue, kept at $15^{o}C$ and examined daily for hatching of nymphs. Enough nymphs were obtained in this way to begin the experiments.

Nymphs were weighed within 24 hours of birth and within 24 hours of the start of each instar. The exuviae produced at the end of each instar were also weighed. On each feeding day a number of aphids of similar size were collected from an A.glutinosa windbreak, weighed and fed to the capsids. On the next feeding day aphids were classified as alive, killed and eaten or dead. Those in each category were weighed, dried to constant weight

and the dry weights obtained. Control batches of live aphids were caged without capsids and classified in the same manner. Not even the largest capsids consumed all the food they received in each two-day period, thus the amount of food provided was considered to be adequate. Occasional dead aphids were found amongst the controls. The numbers of dead specimens found in capsids of instars one to four were also small and not significantly different from the controls. However, in some of the fifth instar cages significantly larger numbers of dead aphids were found and thus these were classified as 'killed' in the manner as by Glen (1973).

Batches of aphids killed by chloroform and left in cages on leaves in the boxes retained 71% of their original weight after two days. It was assumed that aphids in the dead category or those which had been killed and partly eaten lost a similar amount of water and the weights of these were adjusted upwards to allow for water loss. From this the weight consumed was calculated. The aphids which had been killed and consumed were not adjusted for water loss. Almost all of the body fluids were removed and water loss is considered to have been negligible.

Samples of 100 third and fourth instar aphids were killed and dried to constant weight. The dry weight was found to be 32% and 33% respectively of the wet weight. From the dry weight of the remains and the dry weight of the aphid food provided, the dry weight consumed was calculated.

First and second instar capsids were fed third instar aphids and third to fifth instar capsids were given fourth instar aphids (where possible presumptive apterae).

Samples of newly hatched bugs were weighed and dried to constant weight as were newly moulted adults. The increase in dry weight throughout development was found to be 24.6% of the increase in fresh weight; similar

to the figure of 22% quoted by Glen (1973).

6.1.3. Results

The increase in weight of capsids and the amount of aphid material consumed during development is given in table 84. Some mortality of capsids occurred in the first instar. This appeared to be due to waxing of the nymph's head and mouthparts, a defensive response of P.alni. Death may have been caused by starvation or through being unable to shed the old exuvium from the proboscis. Older instars occasionally died through failing to skin change completely. The cause of death could not be established in four other cases.

P.alni appears to represent an acceptable food for B.angulatus and the bugs reared were very similar in weight to those obtained by Glen (1973) using E.tiliae as food. Males were significantly smaller than females at the teneral adult stage. The average weight of males was 1.617 mg and of females 1.964 mg ($t=2.82, d.f.=31, p<0.01$). The cumulative weight of aphids consumed and the increase in body weight are shown in fig.177. Overall, capsids consumed 5.666 mg. of 'wet' aphid material. The proportion of the wet weight of aphids consumed was 70.5%; therefore the total amount of aphid material attacked was 8.041 mg. The average weight of individuals of a given instar of P.alni varies during the year and therefore aphid weights measured over a short period are unlikely to be representative of those over the whole season. Neither is a predator in the field likely to only select aphids of one particular instar. However, to give some idea of the range of numbers of aphids consumed, the figure of total weight of aphids attacked represents 268 first instar aphids or, perhaps more realistically, 115 third instars or 67 fourth instars of the summer generations.

The early instars contributed little to the total food consumption;

Table 84: Increase in weight and weight of P.alni consumed by B.angulatus nymphs at 15°C.

Capsid instar	Number of nymphs	Body weight increase during instar µg	Weight of exuviae µg	Dry weight of aphids consumed µg	% of wet weight of aphids consumed
1	45	76 ± 3	4.2 ± 0.04	37.8 ± 0.6	82.9 ± 0.9
2	40	162 ± 14	5.9 ± 0.03	86.6 ± 1.9	80.6 ± 1.1
3	38	301 ± 21	15.4 ± 0.5	145.8 ± 3.2	78.4 ± 0.9
4	37	583 ± 30	26.5 ± 0.8	334.9 ± 9	75.1 ± 1.1
5 (males	16	442 ± 24	42.3 ± 1.1	673.7 ± 19.4	65.1 ± 2.2
5 (mean					
5 (females	19	704 ± 47			
Overall (males		1534 ± 26	94.4 ± 2.1	1279 ± 27.5	70.5 ± 1.8
Overall (mean					
Overall (females		1881 ± 57			

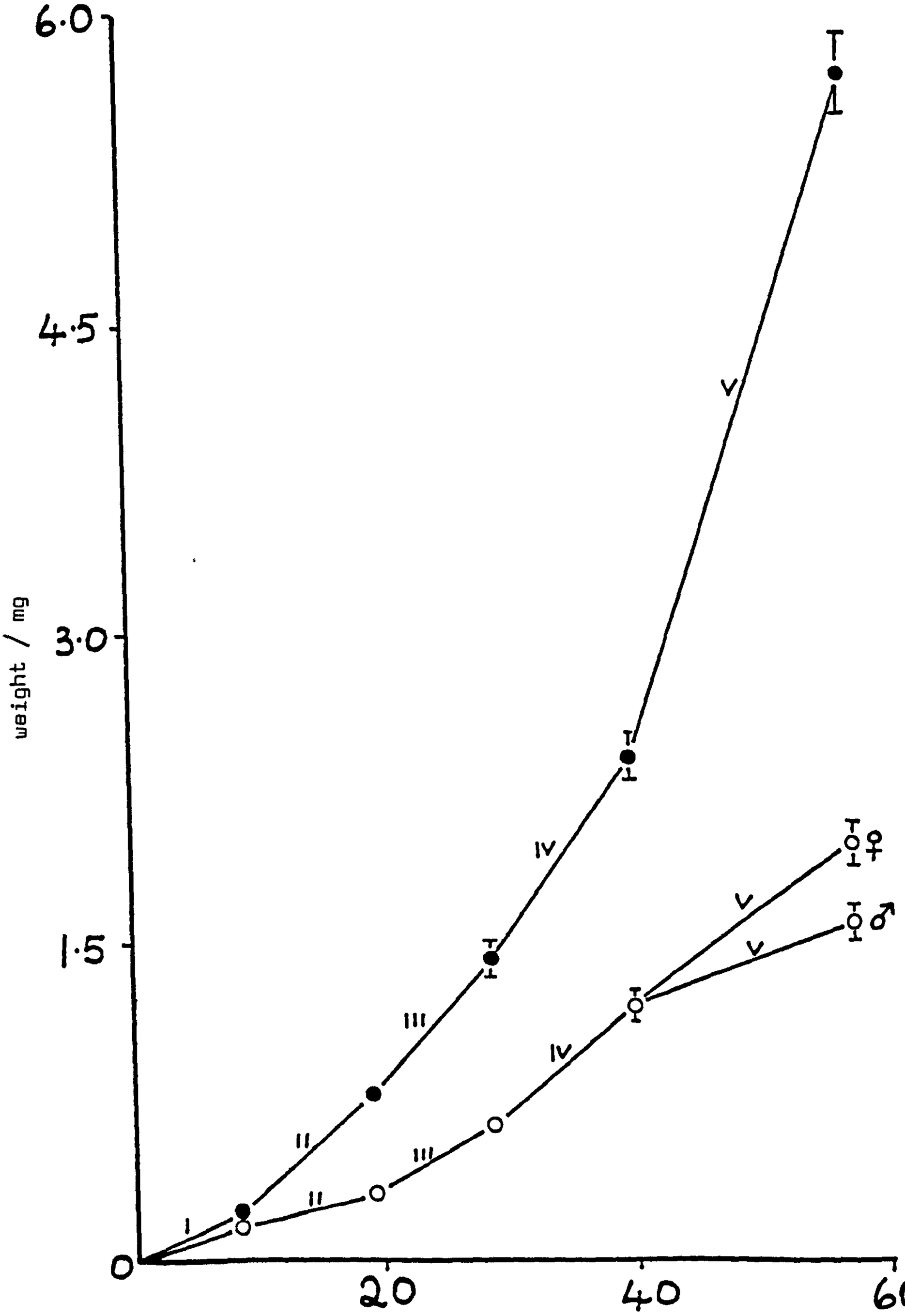


Figure 177: Development of B.angulatus at 15°C, showing length of time in each instar, increase in body weight (O) and the cumulative wet weight of aphids consumed (●).
Roman numerals denote instars.

instars I - III accounted for 25%, instar IV, 20% and instar V,55%.

The efficiency with which food is converted into body weight is measured by the growth efficiency calculated by

$$\text{growth efficiency} = \frac{\text{increase in dry weight}}{\text{dry weight of aphids eaten}} \times 100$$

The growth efficiencies for each instar as well as for the overall development of males and females were calculated and the results are presented in table 85. There were no differences in growth efficiencies of the first three instars; however, that of instar IV was less than that for instar III ($d = 3.69$, $p < 0.001$), and those of instar V were less than instar IV (males, $d=23.95$, $d.f.=43$. $p < 0.001$; females, $d=9.80$, $d.f.=55$, $p < 0.001$). That of males in the fifth instar was significantly less than that of females ($d=15.84$, $d.f.=25$, $p < 0.001$). The overall growth efficiency of males was less than that of females ($t=4.54$, $d.f.=33$, $p < 0.001$)

The growth efficiencies calculated for B.angulatus in the instars I-IV were very similar to the corresponding values obtained by Glen (1973) using E.tiliae as food ($\chi^2_3 = 1.89$, $p > 0.05$).

6.2. FIELD STUDIES

6.2.1. Introduction

The different mortality factors acting upon an insect population may be examined by preparing a life table using counts within a generation of an insect population in the field (Varley, Gradwell and Hassell,1973). Census figures obtained of insects such as aphids which have overlapping generations may be hard to interpret and the construction of a life table difficult. A life table for P.alni is under construction and will be reported elsewhere. Animals with discrete generations are more easily studied in this way.

Table 85: The efficiency with which B.angulatus converts food into body tissue, measured by growth efficiency. Values tabulated are means ± standard error.

B.angulatus instar							
1	2	3	4	5		egg to adult	
				males	females	males	females
n=45	n=40	n=38	n=37	n=16	n=19	n=16	n=19
48.5	46.1	50.8	42.8	12.5	28.1	29.9	37.8
± 1.8	± 1.4	± 1.8	± 1.2	± 0.4	± 0.9	± 1.1	± 1.3

The aim of preparing a life table is to show the effects on a population of successive events in their natural order and to express their numerical effects in a convenient manner. Population counts are inserted into the life table before and after the events occur. If the population figures are converted to logarithms then the effects of the various mortality factors acting on the population can be expressed logarithmically as their killing power or k value. The k value is the difference between the logarithm of the population before and after the mortality acts (Varley et al. 1973). The k values can be added up and since they act in sequence their sum equals the generation mortality, K.

In the examination of life table data key factor analysis has often been used to estimate the contribution of each mortality factor acting on the population to the total mortality (Varley and Gradwell, 1960). The separate mortalities, calculated as k values are plotted against generation number (or for animals with one generation per year, time) and visually compared with the total mortality, K. for as many generations as possible. Often it is possible to identify which submortality is contributing most to the total. This submortality is termed the 'key factor'. Podoler and Rogers (1975) suggested an alternative method whereby the individual k values are plotted on the y axis against the total mortality on the x axis. The regression coefficient for each k value is calculated and the one which gives the greatest value for the slope of the line (b) is, by definition, the key factor.

B.angulatus is an insect which lends itself well to life table analysis, having only one generation per year, overwintering as an egg (Collyer,1952). Glen and Barlow (1980) constructed life tables for the bug on time and investigated the changing effects of prey (lime aphid) numbers on the numbers of the bug.

In this section, life tables for B.angulatus on alder are constructed using detailed census figures obtained through field sampling.

6.2.2. Materials and methods

Counts were made of all instars of B.angulatus recorded in the weekly 200 leaf samples on LF125 and WM110 during 1982,83 and 84. The number of nymphs on the leaves was estimated as the mean number present in the six week period after egg hatch and before numbers declined at maturity. The initial number of adults present was estimated from the mean number present after most nymphs had moulted to adults and before the numbers declined in August. Adults were sexed in the field using the distinctions described by Collyer (1952). The potential egg production calculated using the assumption that each female could lay forty-four eggs (Glen,1973).

The eggs are inserted into twigs with the operculum remaining above the surface. An injury to the wood tissue is formed, causing a small 'bump' which is an aid in counting eggs (Collyer,1952). Bumps do not form in wounds, leaf scars or lenticels and the presence of the egg must then be detected by the white oval rim of the egg cap (illustrated in Collyer,1952). Eggs were counted by examining the twigs associated with 200 leaf scars. The number of eggs in one year was related to the number of nymphs in the following year, using the ratio of leaf scars in year n to leaves in year n + 1 to correct for the increase in leaf number from year to year.

Total generation mortality was calculated starting with the number of eggs in year n and ending with the number of eggs in year n + 1. Individual mortality factors were considered as described by Glen and Barlow (1980). Although not all the factors described by those authors were seen to act in the present study, no different factors were found either.

6.2.3. Results

Life tables for B.angulatus from 1982 - 1984 are presented in table 86 a-e. The importance of the individual mortalities is discussed below.

k_1 - loss of eggs and young nymphs

Compared to the later mortality factors, this was relatively constant. Glen (1975) found that first instar capsids require a prey density for survival nine times that needed from the third instar onwards. In general, when the capsids hatched from the eggs small aphids were plentiful. Even in years such as 1984 on WM110 when aphid numbers began to increase during June, only the earliest emerging bugs in early June may have had trouble finding food. There was a tendency for k_1 to be higher in years when aphids were scarce in June, suggesting some mortality of these capsid nymphs (table 86 c-e). Nymphs were also observed on the leaves one or two weeks later in 1984 than in 1982 or 1983 and this may have been due to death through starvation of the earliest hatchlings.

k_2 - parasitism

First and second B.angulatus are parasitized by a braconid, Peristenus malatus Loan (Glen,1977b). Parasitized fifth instar nymphs are easily recognised in the field by their greatly swollen abdomens. Only in 1983 on WM110 section 3 were a few parasitized specimens found but these did not contribute greatly to the overall mortality.

k_3 - fungal disease

Glen and Barlow (1980) noted some individuals killed by Entomophthora spp. but none were found in the course of this study.

Table 86 (a): Life table for B.angulatus on LF125, section 1

		1981 - 1982			1982 - 1983			1983 - 1984		
		Number alive/200 leaves	log.no. alive	k value	Number alive/200 leaves	log.no. alive	k value	Number alive/200 leaves	log.no. alive	k value
	Number of eggs	20.47	1.311		23.77	1.376		52.24	1.718	
k_1	Loss of eggs/young nymphs	6.33	0.802	o.509	11.75	1.070	0.306	19.82	1.297	0.421
k_2	Parasitism	6.33	0.802		11.75	1.070		19.82	1.297	
k_3	Fungal disease	6.33	0.802		11.75	1.070		19.82	1.297	
k_4	Loss of old nymphs/young adults	6.03	0.781	0.021	4.28	0.631	0.439	11.48	1.060	0.237
k_5	Early migration of males	4.94	0.694	0.087	5.04	0.607	0.024	7.93	0.899	0.161
k_6	Eggs not laid	4.16	0.619	0.075	1.86	0.269	0.338	1.54	0.188	0.711
k_7	Increase in leaves from year to year	3.52	0.546	0.072	1.58	0.200	0.069	1.31	0.117	0.071
Total K				0.764			1.176			1.400

Table 86 (b): Life table for B.angulatus on LF125, section 2

	1982 - 1983			1983 - 1984		
	Number alive/200 leaves	log.no. alive	k value	Number alive/200 leaves	log.no.	k value
Number of eggs	25.66	1.409		24.14	1.383	
k_1 Loss of eggs/young nymphs	9.71	0.987	0.422	16.40	1.215	0.168
k_2 Parasitism	9.71	0.987		16.40	1.215	
k_3 Fungal disease	9.71	0.987		16.40	1.215	
k_4 Loss of old nymphs/young adults	5.55	0.744	0.243	7.96	0.901	0.314
k_5 Early migration of males	4.08	0.611	0.133	6.31	0.800	0.101
k_6 Eggs not laid	2.11	0.324	0.286	2.64	0.422	0.378
k_7 Increase in leaves from year to year	1.79	0.254	0.070	2.24	0.351	0.071
Total K			1.155			1.032

Table 86 (c) : Life table for B.angulatus on WM110, section 1

		1981 - 1982			1982 - 1983			1983 - 1984		
		Number alive/200 leaves	log.no. alive	k value	Number alive/200 leaves	log.no. alive	k value	Number alive/200 leaves	log.no. alive	k value
	Number of eggs	5.80	0.763		7.13	0.853		5.02	0.701	
k_1	Loss of eggs/young nymphs	3.33	0.522	0.241	4.50	0.653	0.200	3.15	0.498	0.203
k_2	Parasitism	3.33	0.522		4.50	0.653		3.15	0.498	
k_3	Fungal disease	3.33	0.522		4.50	0.653		3,15	0.498	
k_4	Loss of old nymphs/young adults	3.16	0.501	0.021	3.52	0.547	0.106	3.05	0.485	0.013
k_5	Early migration of males	1.87	0.271	0.230	3.04	0.483	0.064	1.74	0.240	0.245
k_6	Eggs not laid	1.44	0.160	0.111	1.52	0.181	0.302	1.26	0.101	0.139
k_7	Increase in leaves from year to year	1.23	0.090	0.070	1.29	0.111	0.070	1.08	0.033	0.068
Total K				0.673			0.742			0.668

Table 86 (d): Life table for B.angulatus on WM110, section 2

	1982 - 1983			1983 - 1984		
	Number alive/200 leaves	log.no. alive	k value	Number alive/200 leaves	log.no. alive	k value
Number of eggs	4.03	0.606		9.88	0.995	
k_1 Loss of eggs/young nymphs	3.11	0.493	0.113	4.00	0.602	0.393
k_2 Parasitism	3.11	0.493		4.00	0.602	
k_3 Fungal disease	3.11	0.493		4.00	0.602	
k_4 Loss of old nymphs/young adults	2.45	0.389	0.104	3.35	0.525	0.077
k_5 Early migration of males	2.05	0.312	0.077	2.07	0.316	0.209
k_6 Eggs not laid	1.37	0.136	0.176	1.40	0.147	0.169
k_7 Increase in leaves from year to year	1.16	0.064	0.072	1.19	0.078	0.069
Total K			0.542			0.917

Table 86 (e): Life table for B.angulatus on WM110, section 3

	1981 - 1982			1982 - 1983			1983 - 1984		
	Number alive/200 leaves	log.no. alive	k value	Number alive/200 leaves	log.no. alive	k value	Number alive/200 leaves	log.no. alive	k value
Number of eggs	4.27	0.631		22.30	1.349		8.67	0.938	
k_1 Loss of eggs/young nymphs	3.17	0.501	0.130	12.75	1.106	0.243	4.33	0.637	0.301
k_2 Parasitism	3.17	0.501		12.36	1.092	0.014	4.33	0.637	
k_3 Fungal disease	3.17	0.501		12.36	1.092		4.33	0.637	
k_4 Loss of old nymphs/young adults	2.55	0.407	0.094	6.03	0.780	0.312	3.85	0.586	0.051
k_5 Early migration of males	2.02	0.305	0.102	4.78	0.679	0.101	2.29	0.361	0.225
k_6 Eggs not laid	1.28	0.107	0.198	1.89	0.278	0.401	1.46	0.164	0.197
k_7 Increase in leaves from year to year	1.09	0.037	0.070	1.62	0.209	0.069	1.25	0.097	0.067
Total K			0.594			1.140			0.841

k_4 - loss of old nymphs and young adults

This was high on occasions when the aphid population peaked early in the year, well before the bugs became adult. Such an event occurred on LF125 in 1983 and 1984. This may have been caused by starvation of fifth instar capsids, unable to find food. However, at the time when the capsids were at this age, adults were still quite numerous, although more so in 1984 (an average of 0.66 aphids per leaf in 1983; 4.9 per leaf in 1984). A more likely explanation is that adults were migrating from the windbreak as soon as they became mature, due to prey becoming scarce. This was supported by the sticky trap catches in both years. Adults were recorded upon these the week following their first appearance on the windbreak.

k_5 - early migration of males

When aphids were relatively common on the windbreak during August, males appeared to emigrate before females, shown by their disappearance from the alder and their appearance on the sticky traps. Such an event occurred from WM110 in 1984. Aphids were present throughout August and male capsids left in mid August; females not doing so until early September. Glen and Barlow (1980) observed a similar occurrence on lime and tested bug flight in the laboratory. It was found that male capsids flew before females when aphids were plentiful. When aphids were sparse, both sexes flew in equal quantities. Although not tested under controlled conditions, it appears that a similar event happened on the windbreaks. When the aphid population declined early, males and females flew together and k_5 was relatively low. Examples are provided by LF125 sections 1 and 2 in 1983 and 1984 (table 86a,b).

k_6 - eggs not laid

This was due to the death or emigration of females before they had laid their full egg complement. When aphids were present at bug egg laying

time, females tended to remain upon the windbreak and k_6 was relatively low. Examples are all three sections of WM110 in 1984. However if aphids were scarce or even absent during the early oviposition period females left the alder with the males and k_6 was relatively high (e.g. WM110, all sections, 1983), (table 86 c-e). It is interesting to note that not all females left the windbreak. Even in years such as 1983 when bug migration began in late July, adult females were still found well into September and even October on some sections. On some sampling occasions, no aphids were found on the 200 leaves examined but bugs were plentiful (an average of 0.2 per leaf). This prevented k_6 from being higher than it might have been and also ensured a supply of eggs for the following season.

k_7 - increase in leaves

This was accounted for because 200 leaf scars does not represent 200 leaves the following season. The egg count was adjusted to correct for the 'increase' in leaves. The values of k_7 were small and insignificant in every case examined and contributed little to the total mortalities.

It is clearly meaningless to plot the k values obtained from the windbreaks against generation number as lines with two or three points would show very little. Podoler and Rogers (1975) stated that variations in the contributions of the k values could occur from one area to another. Accepting that this could apply to the different windbreaks studied here, the test of Podoler and Rogers was applied to the data in an attempt to determine which was the key factor affecting changes in numbers of B.angulatus. Each k value was plotted on the y axis and the total on the x axis (fig.178). Parasitism was omitted, having only one point. The regression coefficients for each line are listed in the figure. It is clear that the key factor is k_6 - the loss of adult females as this is the k value with the largest regression coefficient.

Figure 178:

Podoler and Rogers' (1975) test for key factors:

(a) k_1, Loss of eggs/young nymphs

$y = 0.124x + 0.155$

$r = 0.2789$, d.f. = 11. $p > 0.05$

(b) k_4, Loss of old nymphs

$y = 0.395x - 0.197$

$r = 0.7597$, d.f. = 11, $p < 0.01$

(c) k_5, Early migration of males

$y = -0.039x - 0.171$

$r = 0.8152$, d.f. = 11, $p > 0.05$

(d) k_6, Eggs not laid

$y = 0.517x - 0.196$

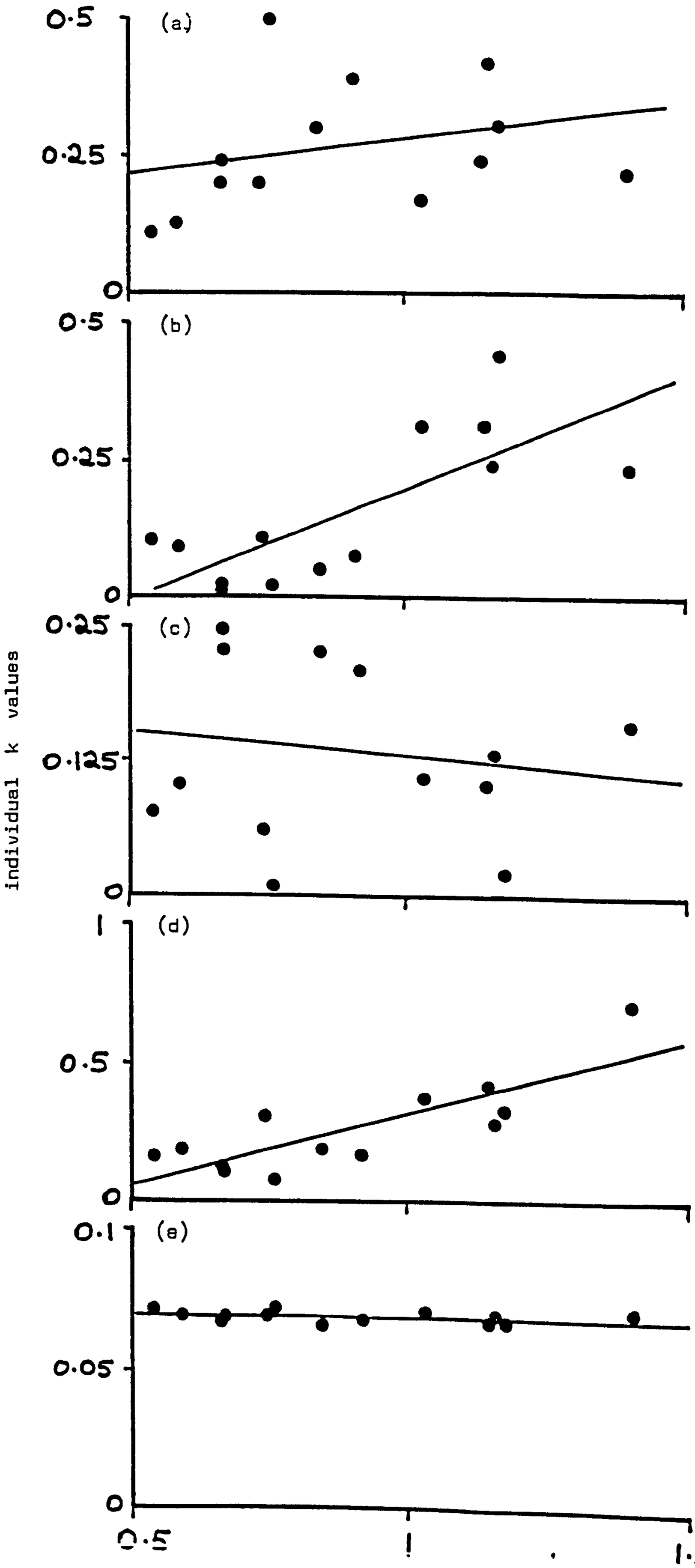
$r = 0.8152$, d.f. = 11, $p < 0.001$

(e) k_7, Increase in leaves from year to year

$y = 0.0000032x + 0.069$

$r = 0.00057$, d.f. = 11, $p > 0.05$

By definition, k_6 is the key factor as it has the largest regression coefficient (0.517).


(a)
0·5
0·25
0
(b)
0·5
0·25
0
(c)
0·25
0·125
0
individual k values
(d)
1
0·5
0
(e)
0·1
0·05
0
0·5
1
1·5

The next largest is k_4, the loss of old nymphs and young adults. This is a likely result of most aphid populations reaching their peak before the bugs were adult, but this factor may also be influenced by windbreak pruning. The only other significant factor is k_1, the loss of eggs and young nymphs. It is not known to what extent B.angulatus eggs are predated on during winter. Possible enemies are anthocorid bugs which may be active on warm days, (Hill,1957). The most likely cause of this mortality is the death of young nymphs which may starve due to the lack of aphid prey in years when fundatrix numbers are extremely low.

In only two cases out of the eight examined did the number of capsid nymphs decrease from one year to the next (fig.179). These two instances were on WM110 section 1 1983-1984 and WM110 section 3 1983-1984. On both of these sections aphid numbers in the leaf samples fell to zero for periods of time (chapter 2) and it is likely that the extreme lack of prey caused many female bugs to migrate. No bugs were recorded in leaf samples on section 1 or 3 after September 22nd, but bugs continued to be found on section 2 until mid October. Aphid numbers did not fall to zero on section 2 and as a result more eggs were laid and numbers were higher in 1984. Therefore it appears that a certain number of female capsids remain upon the windbreak if there is some prey available. When aphid prey is present even in as low a density of 0.001 per cm^2, capsids increased in numbers by a constant percentage:

$$y = 1.29x$$

$$(r = 0.980, d.f. = 4,\ p < 0.001),$$

where y is the cumulative number of immature capsids in year n + 1 and x the number in year n. There were only two points whereby the number of capsids decreased from one year to another. Any relationship must be suspect, but a calculated line gives $y = 0.33x$ (fig.179). If this relationship is true, then theoretically it would take B.angulatus five years to recover its numbers following a poor year for egg laying.

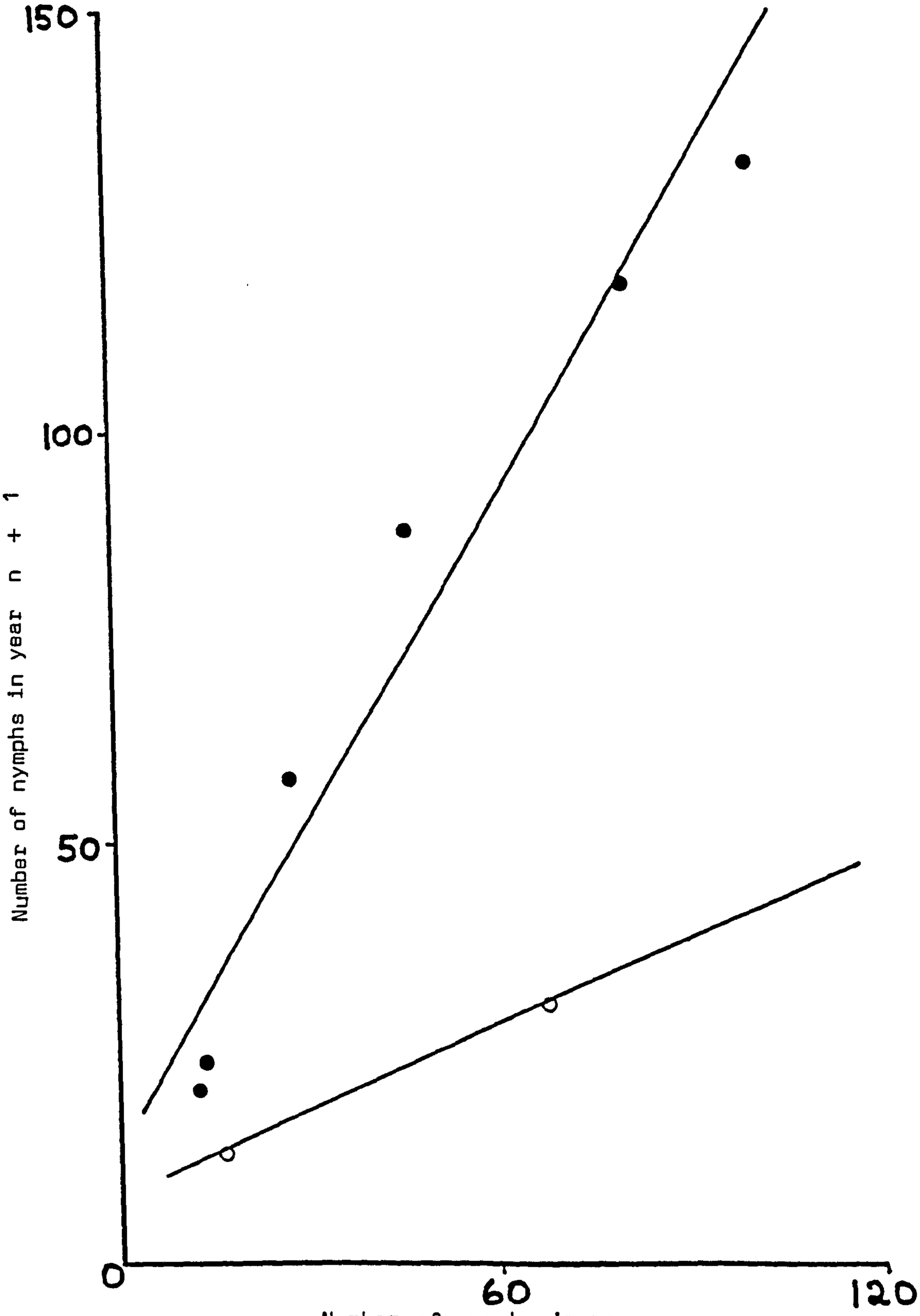


Figure 179: The relationship between the cumulative number of B.angulatus nymphs in year n to that of the following year.

● y = 1.29x + 12.60

○ y = 0.33x + 8.33

6.3. MIGRATION OF B.ANGULATUS

6.3.1. Introduction

Muir (1966b) found that adult B.angulatus colonized apple orchards and ware effective in reducing numbers of the fruit tree red spider mite, P.ulmi. Solomon(1975b) reported that capsid adults colonized orchards by movement from nearby windbreaks of alder and this was also suggested by Skinner (1983) using sticky trap catches. The migration of B.angulatus is examined in this section in an attempt to relate this to aphid numbers on the alder.

6.3.2. Materials and methods

All capsid instars were counted weekly in the 200 leaf samples. Flight within the canopy, from the windbreak and in the orchard, was measured by sticky trap catches used to record aphid flight (described in chapter 3).

6.3.3. Results

The aphid and capsid numbers on the windbreak and bug migration from it are shown in figs.180-183. On each windbreak bugs appeared at a similar time in each year, from mid June onwards. Migration, however, did not occur at a similar time within years and appeared to be closely related to the abundance of aphids. On LF125 (fig.180) capsid numbers were low on the leaves throughout late summer 1982. Aphids were sparse due to the spraying earlier in the season but were generally present in at least some numbers. Bug migration appeared to be insignificant and the numbers of capsids stayed very constant after an initial small early migration. Sufficient bugs remained to deposit enough eggs to increase the numbers in 1983. In 1983 initial aphid numbers were high and the populations peaked early. The result was that the aphid numbers were declining

Figure 180:

Numbers of P.alni and B.angulatus on the windbreak and capsid migration from it.

(a) LF 125 section 1, 1982

(b) LF 125 section 1, 1983

(c) LF 125 section 2, 1983

(d) LF 125 section 1, 1984

(e) LF 125 section 2, 1984

——— P.alni populations

-- - - - B.angulatus numbers

Histograms represent capsid migration measured by numbers on sticky traps.

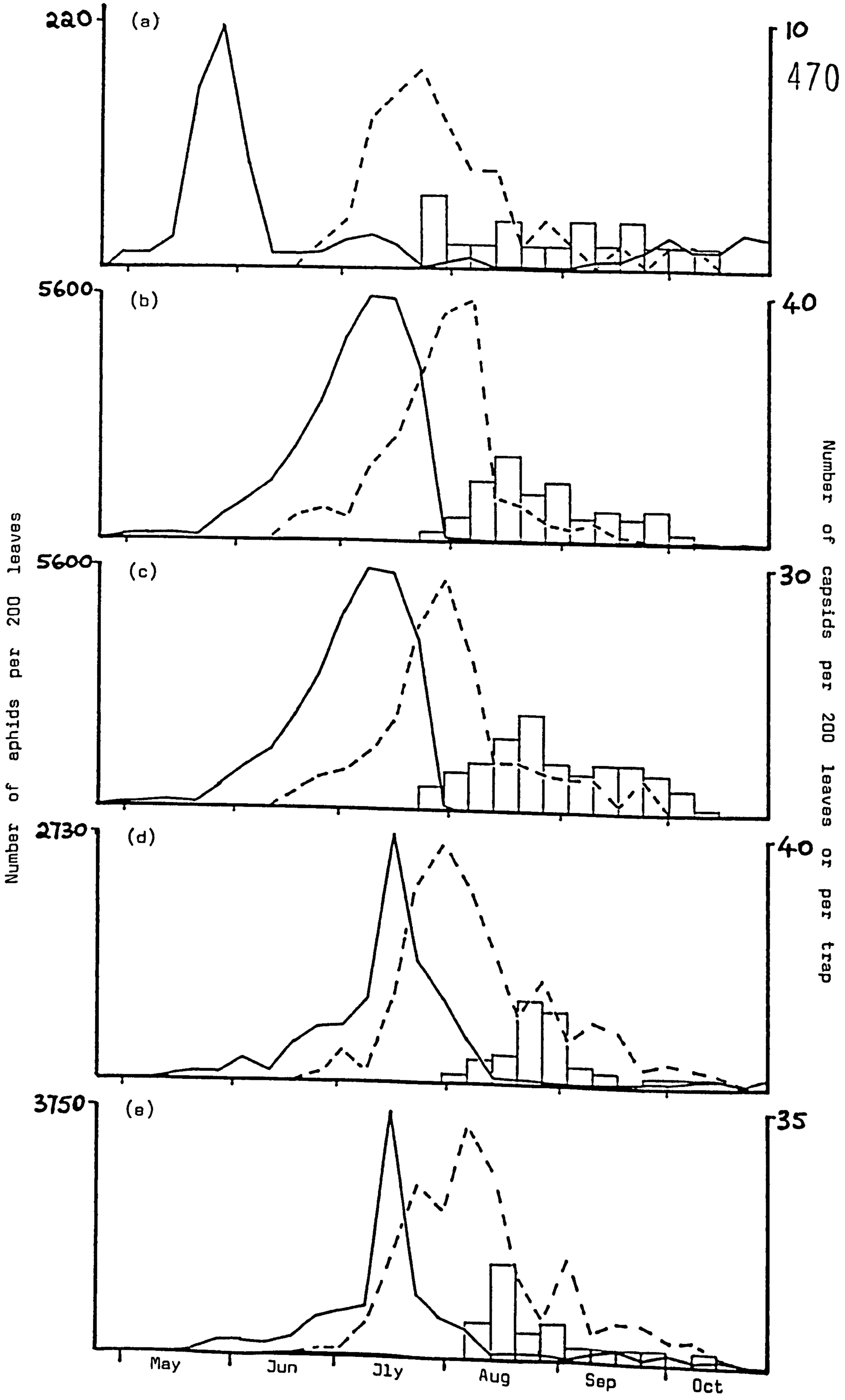

220
(a)
10
470
5600
(b)
40
5600
(c)
30
2730
(d)
40
3750
(e)
35
May
Jun
Jly
Aug
Sep
Oct
Number of aphids per 200 leaves
Number of capsids per 200 leaves or per trap

Figure 181:

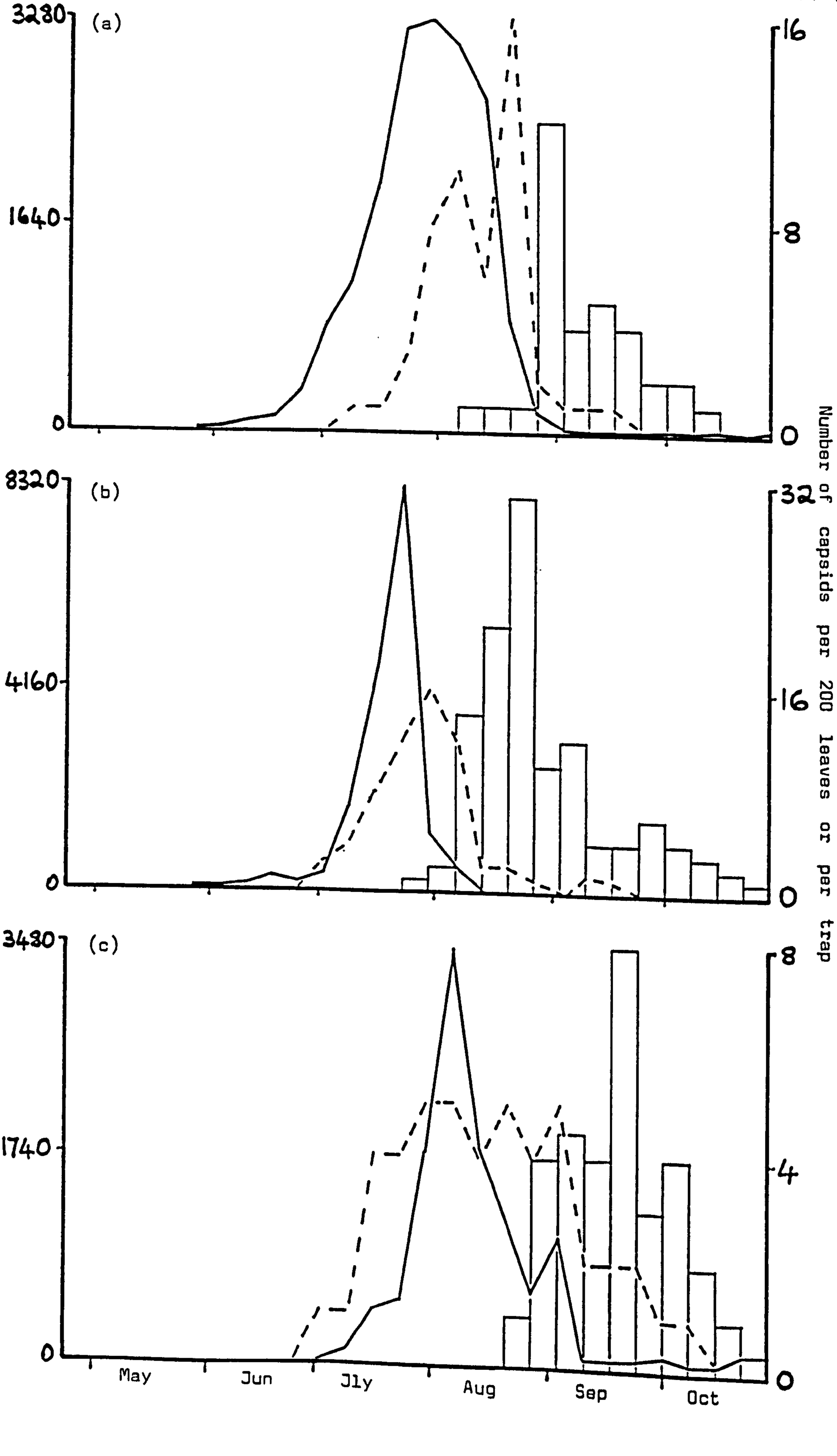
Numbers of P.alni and B.angulatus on the windbreak and capsid migration from it:

(a) WM 110 section 1, 1982

(b) WM 110 section 1, 1983

(c) WM 110 section 1, 1984

For key, see figure 180


(a)
3280
1640
0
16
8
0
(b)
8320
4160
0
32
16
0
(c)
3480
1740
0
8
4
0
May
Jun
Jly
Aug
Sep
Oct
Number of aphids per 200 leaves
Number of capsids per 200 leaves or per trap

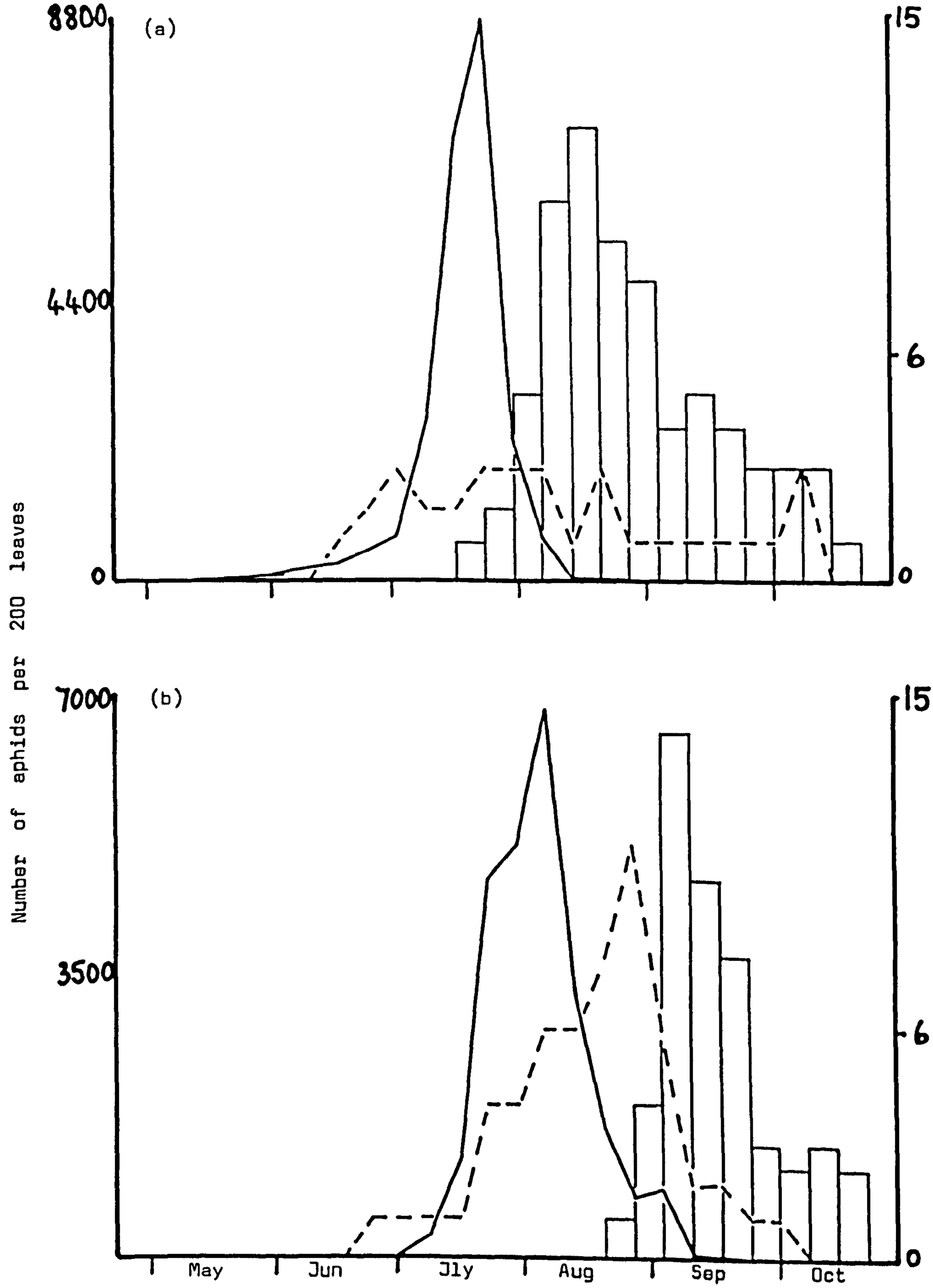


Figure 182: Numbers of P.alni and B.angulatus on the windbreak and capsid migration from it:

(a) WM 110 section 2, 1983

(b) WM 110 section 2, 1984

For key, see figure 180

Figure 182 cont.

(c) WM 110 section 2, 3.5m 1983

(d) WM 110 section 2, 7.5m 1983

(e) WM 110 section 2, 3.5m 1984

(f) WM 110 section 2, 7.5m 1984

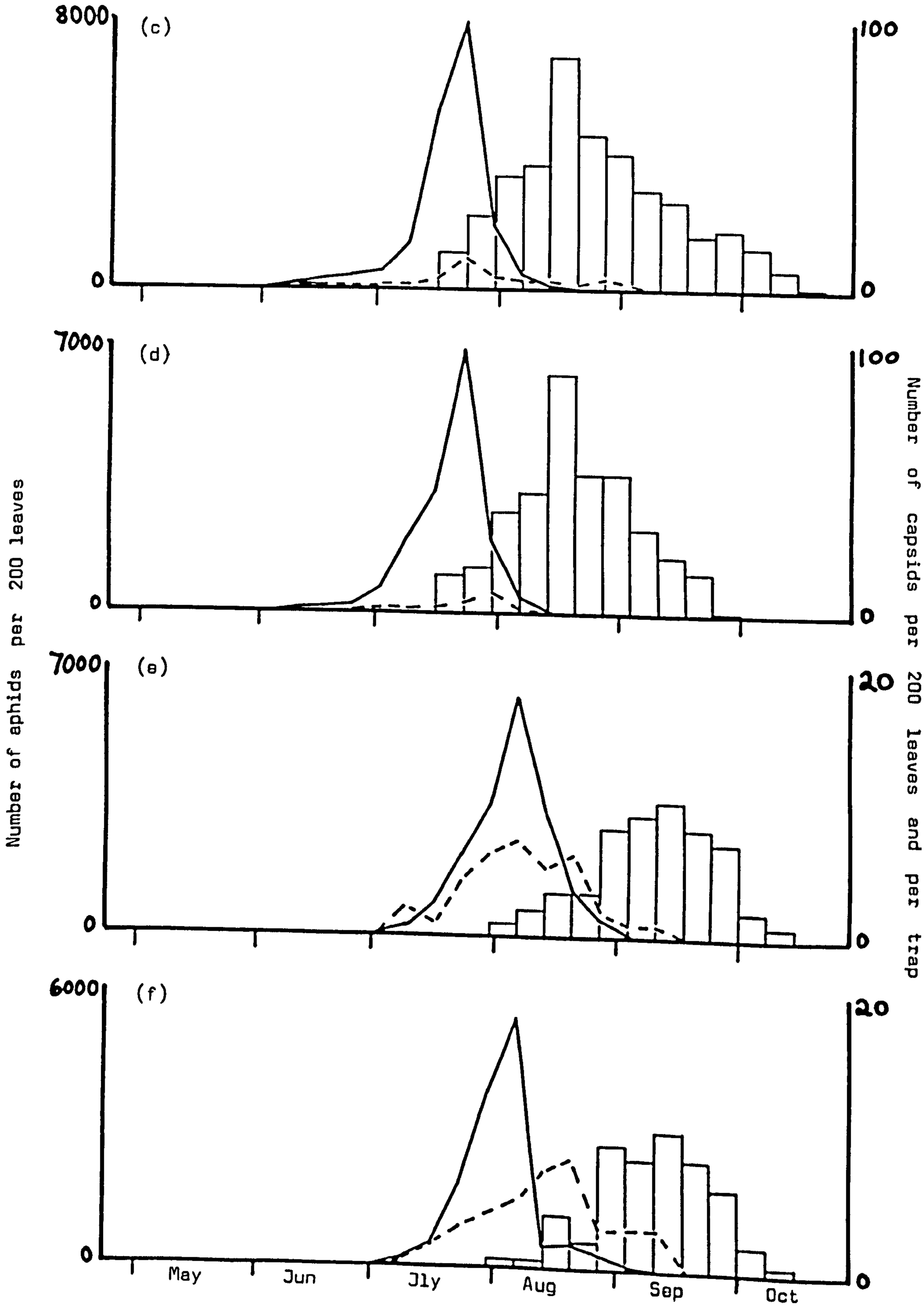

8000
(c)
0
100
0
7000
(d)
0
100
0
Number of capsids per 200 leaves
7000
(a)
0
20
0
Number of aphids
200 leaves and per tra
6000
(f)
0
20
0
May
Jun
Jly
Aug
Sep
Oct

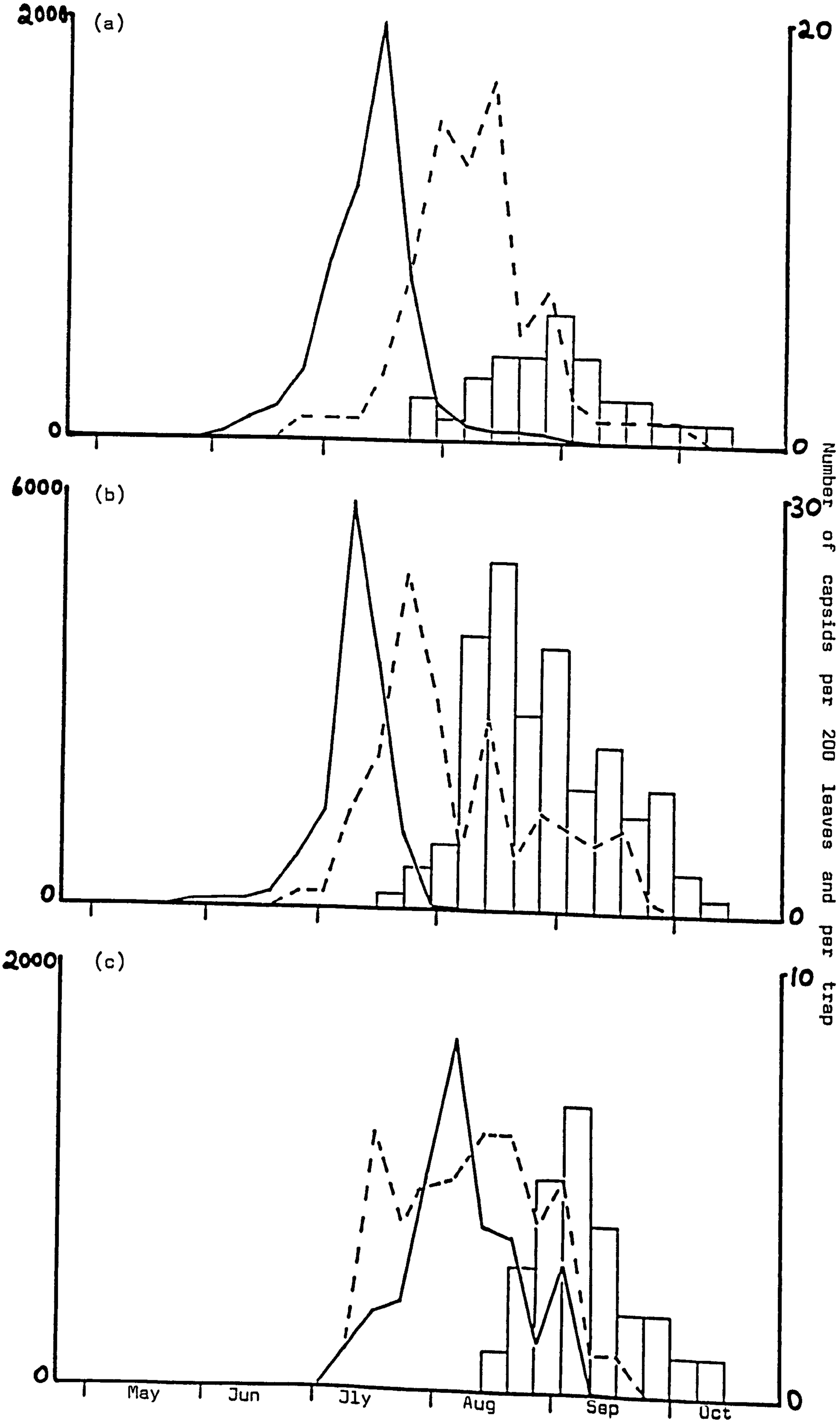
Figure 183: Number of P.alni and B.angulatus on the windbreak and capsid migration from it:

(a) WM 110 section 3, 1982

(b) WM 110 section 3, 1983

(c) WM 110 section 3, 1984

For key, see Figure 180


2000
(a)
0
20
0
Number of capsids per trap
6000
(b)
0
30
0
Number of aphids per 200 leaves
Number of capsids per 200 leaves and per trap
2000
(c)
0
10
0
May
Jun
Jly
Aug
Sep
Oct

rapidly when the bugs were becoming adult and migration occurred early in adult life, resulting in a relatively high value of k_4 (table 86a). Some aphids remained however as did some female capsids and enough eggs were laid for the population to increase in 1984. In 1984 a similar event happened. The peak in aphid numbers occurred a week later and bug migration was also a week later. The pattern was generally the same as in 1983.

Differences in migration between years may perhaps be most clearly seen on WM110 (figs.181-183). In 1983 when aphids were numerous in spring the populations peaked early and bug migration was earlier than in 1982 or 1984. The migration in 1983 from sections 1 and 3 continued into mid October and appeared to result in a substantial loss of females and therefore eggs, as numbers of capsid nymphs on these sections in 1984 were lower than in 1983. On section 2 in 1983 the aphids did not disappear completely and although capsid migration continued into October, numbers increased in 1984 so relatively more females must have remained to lay eggs. Section 1 provides a good example of how capsid migration appears to be closely related to changes in aphid abundance. In 1982 aphid numbers peaked on July 29th; bug migration began on August 5th and peaked on August 26th. In 1983 aphid numbers peaked on July 21st. Bug migration began on July 21st and peaked on August 18th. Finally in 1984 aphid numbers peaked on August 2nd. Bug migration began on August 16th and peaked on September 13th. Not only is the flight of capsids related to the time when aphid populations decline but also to their abundance following the period of peak numbers. Although aphid populations peaked at similar times in 1982 and 1984, the decline was faster in 1982, more aphids remaining on the leaves during August 1984. Capsids remained upon the windbreak for longer in 1984 and migration was delayed compared to 1982. It is unlikely that the capsids themselves caused the more rapid decline in 1982. The cumulative number of nymphs recorded in the two years was identical and the total number of adults greater by only two.

The sticky traps placed within the tree canopy showed similar patterns of bug flight to those traps placed at the orchard edge (fig.182). In 1983 canopy traps caught considerably more bugs than those near the orchard. Numbers caught in 1984 were similar between both sets of traps and considerably less than in 1983. The smaller numbers caught in 1984 are a likely result of the scarcity of capsids in that year due to the migration of females and loss of eggs in 1983. Graphs of the number of bugs caught on orchard traps against those on scaffold traps are depicted in figs.184 and 185. They bear a similarity to those depicting aphid flight in the two years (figs.139 and 140). In both years there is a good correlation between the numbers caught on each trap. The higher numbers on the canopy traps indicate that a considerable amount of intracanopy flight took place, presumably due to the searching of adults for food when prey became scarce. When prey numbers became so low as to be almost absent migration took place. The high numbers on the canopy traps probably represents a number of bugs trying to leave the windbreak. In contrast, in 1984, the slope of the regression lines at each height was not significantly different from 1 (3.5m, $t=1.03, p > 0.05$; 7.5m, $t=0.87, p > 0.05$) indicating that canopy and orchard traps caught similar numbers of bugs. With prey being more abundant, flight in search of food was not necessary and most food probably was caught by active running. Only when prey numbers fell later in the season did bugs migrate and these were mostly males (shown by the relatively high value of k_5, table 86c).

6.4. BUG FLIGHT IN THE ORCHARD

6.4.1. Introduction

Skinner (1983) found that B.angulatus formed a greater percentage of the predators caught on sticky traps at the orchard edge rather than amongst the orchard trees. However, as the orchards in which Skinner worked were insecticide-free, it may be that the increased percentage of capsids caught

Figure 184 :

Relationships between the weekly sticky trap catches of adult capsids in the tree canopy and those caught at the orchard edge:

(a) 3.5m, 1983

regression line: $y = 0.139x + 0.422$

$r = 0.916$, d.f. = 12, $p < 0.001$

(b) 7.5m, 1983

regression line: $y = 0.127x + 1.391$

$r = 0.921$, d.f. = 12, $p < 0.001$

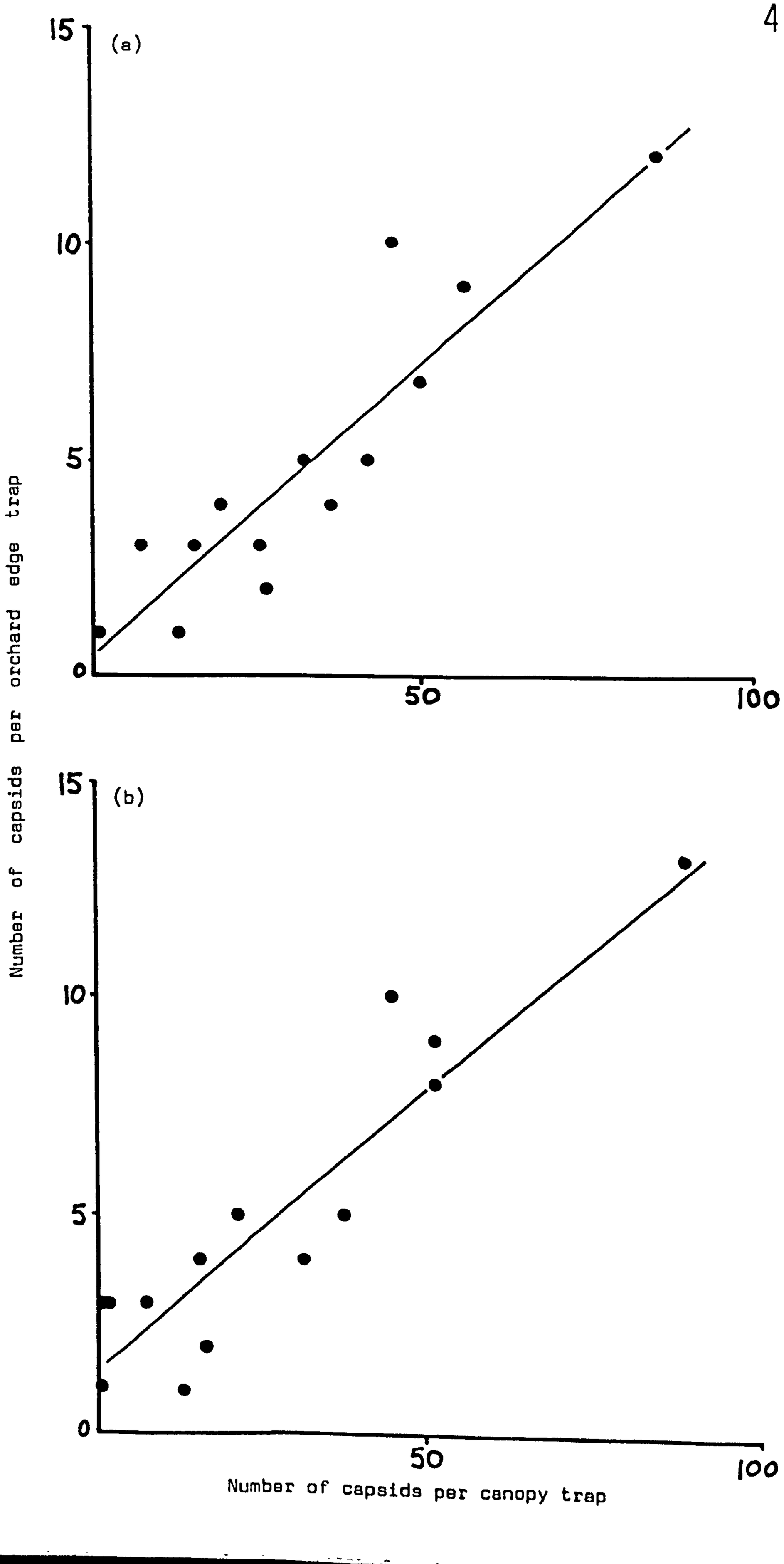

(a)
15
10
5
0
50
100
per orchard edge trap
(b)
15
10
5
0
50
100
Number of capsids per canopy trap
Number of capsids per canopy trap

Figure 185:

Relationship between the weekly sticky trap catches of adult capsids in the tree canopy and those caught at the orchard edge:

(a) 3.5 m, 1984

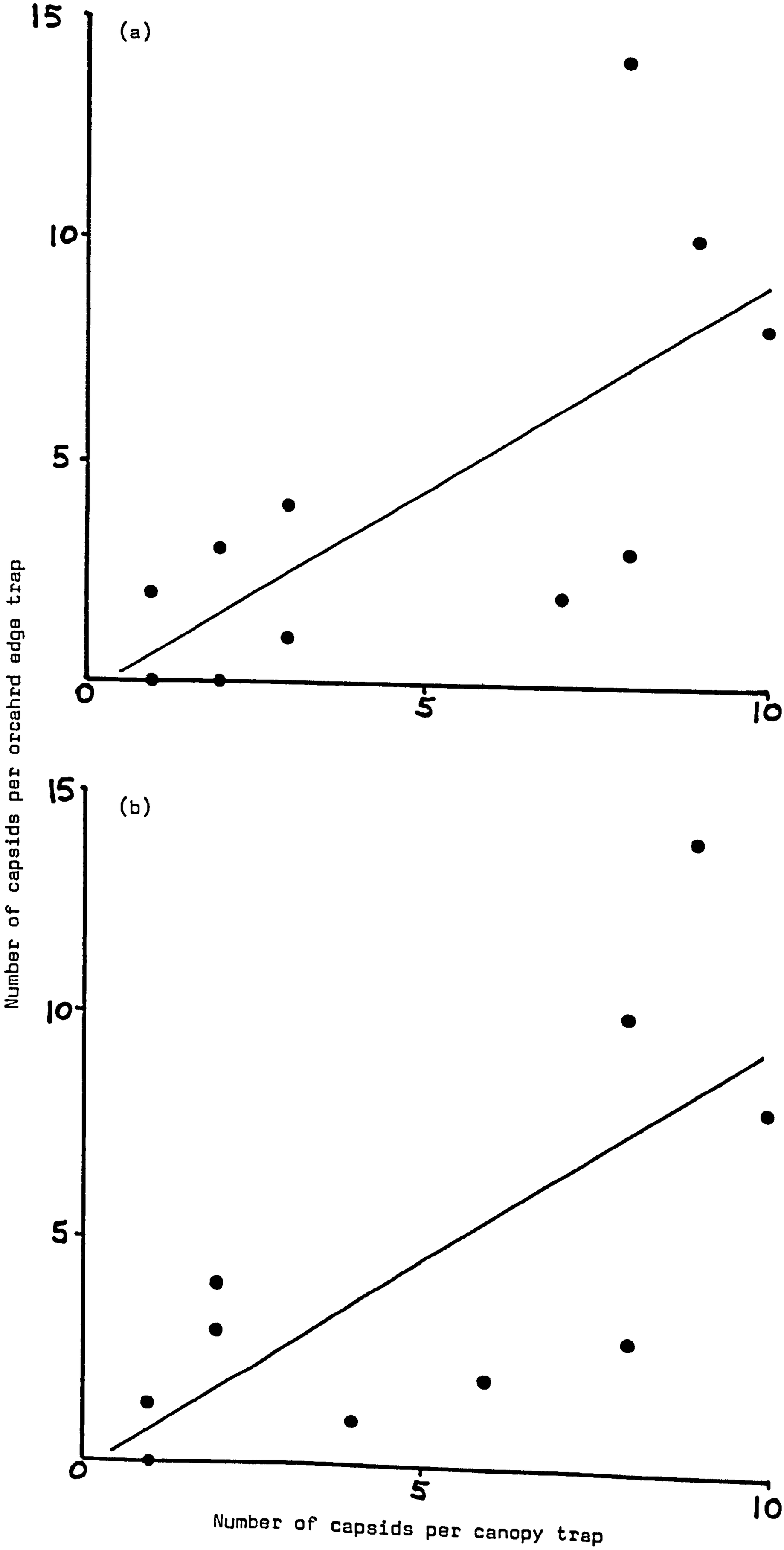
regression line: $y = 0.929x - 0.286$

$r = 0.718$, d.f. = 9, $p < 0.05$

(b) 7.5 m, 1984

regression line: $y = 0.949x - 0.216$

$r = 0.750$, d.f. = 9, $p < 0.01$


(a)
15
10
5
0
5
10
Number of capsids per orcahrd edge trap
(b)
15
10
5
0
5
10
Number of capsids per canopy trap

at the edge was due to bugs emigrating from the orchard rather than immigrating into it from nearby alder. Skinner also found greater numbers of predators on traps amongst the orchard trees. In this work the orchard adjacent to the alder windbreak received a spray programme of insecticides and acaricides, including 'Zolone' (phosalone), carbaryl, 'Secis' (deltamethrin), 'folimat' (omethoate) and 'mitac' (amitraz) None of these chemicals can be considered completely 'safe' against beneficial orchard insects (Anon.,1983). The orchard was thus virtually insect and mite free. Predator flight was examined at the orchard edge and amongst the trees.

6.4.2. Materials and methods

Sticky traps were placed in the orchard 20m from WM110 in 1983 and 1984 (fig.1). Predator numbers were recorded upon these and on those used to record aphid flight at the orchard edge. All traps were examined and renewed weekly.

6.4.3. Results

The relative abundance of the predators recorded on the traps is given in table 87. In 1983, B.angulatus was the commonest predator recorded on the orchard edge traps comprising 44% of numbers caught, significantly more than the 29% caught on the orchard traps ($\chi^2 = 15.94$, $p < 0.001$). However, on the traps within the orchard the commonest predator was C.carnea, the common green lacewing. In this respect these results are similar to those of Skinner (1983) in that edge traps caught a higher percentage of B.angulatus adults. It should be noted that 1983 was a year of high bug migration from WM110 caused by early peaking aphid numbers (figs.181-183). These results therefore support the suggestion that the greater percentage catch of B.angulatus adults on edge traps

Table 87 (a): Total numbers of predators recorded weekly on orchard edge sticky traps, WM110, 1983 (six traps used)

Date	B.angulatus	M.chlorizans	O.marginalis	Anthocorids	Neuroptera	Coccinellidae	Others
2/6				1			
9/6			1			2	
16/6			6				
23/6			5				1
30/6			2			1	
7/7			3	1			
14/7		6	2		6		
21/7	4	20			19	1	
28/7	15	36			13	1	
4/8	27	190		1	20		1
11/8	91	262		1	10		
18/8	110	81			9	1	
25/8	111	79			10		1
1/9	413	30			22		
8/9	129	13			28		
15/9	40	10			40		
22/9	46	20			80		
29/9	73	9			69		
6/10	88	25			158		
13/10	25	10			112		
20/10	2				86		
27/10							
Total	1174	791	19	4	682	6	3
%	43.8	29.5	0.70	0.10	25.5	0.20	0.10

Table 87 (b): Total numbers of predators recorded weekly on sticky traps placed within orchard, 20m from windbreak WM110, 1983 (four traps used)

Date	B.angulatus	M.chlorizans	O.marginalis	Anthocorids	Neuroptera	Coccinellidae	Others
2/6				1		1	
9/6			1				
16/6			2				
23/6			1				
30/6			1			1	
7/7			1				
14/7		1			1		1
21/7	1	2			1	1	
28/7	4	10					
4/8	20	32		1	3		
11/8	26	66			4		
18/8	47	22			2		
25/8	50	24			8	1	
1/9	60	14			11		
8/9	10	12			14		
15/9	19	12			38		
22/9	15	8			61		
29/9	23	5			52		
6/10	20	28			141		
13/10	4				90		
20/10					84		
27/10							
Total	309	236	6	2	510	4	1
%	28.9	22.1	0.5	0.2	47.8	0.4	0.1

Table 87 (c): Total numbers of predators recorded weekly on orchard edge sticky traps,WM 110, 1984 (six traps used)

Date	B.angulatus	M.chlorizans	O.marginalis	Anthocorids	Neuroptera	Coccinellidae	Others
7/6							
14/6							
21/6			1				
28/6			2				
5/7					1		
12/7					1		
19/7					4		
26/7					1		
2/8		3			13		
9/8		21			19	1	
16/8	4	43			31	2	
27/8	9	72			40	1	
30/8	15	81			29	1	
6/9	30	242			37	1	
13/9	35	227			16	1	
20/9	39	13			13		
27/9	12	14			4	1	
5/10	7	8			21		1
12/10	5	7			33		3
19/10							
26/10							
Total	156	731	3	0	263	8	4
%	13.4	62.7	0.3	0.0	22.6	0.7	0.3

Table 87 (d) : Total numbers of predators recorded weekly on sticky traps placed within orchard,20m from WM110, 1984 (four traps used)

Date	B.angulatus	M.chlorizans	O.marginalis	Anthocorids	Neuroptera	Coccinellidae	Others
7/6							
14/6							
21/6			1				
28/6			2				
5/7			1				
12/7			1				
19/7					1		
26/7					1		
2/8					3		
9/8	1				4		
16/8	6	36			1	1	
27/8	3	74			10	2	
30/8	22	81			13	2	
6/9	7	40			11		
13/9	9	28			14		
20/9	9	22			7		
27/9	5	26			5		
5/10	6	8			10		
12/10	1				37		1
18/10							
26/10							
Total	69	315	5	0	117	5	1
%	13.5	61.5	0.9	0.0	22.9	0.9	0.2

is due to migration from nearby alder. Bugs could not have been emigrating from the orchard, due to the spray programme. In contrast to Skinner, the average number of predators caught per trap was highest on the edge traps (447 per trap compared to 267 per trap). This is a likely result of the orchard spraying, meaning that few predators existed within the orchard. Those that were caught there are likely to have been migrants. The delicate apple capsid Malcocoris chlorizans (Panzer) occurred in large numbers on both sets of traps and was second only to B.angulatus on edge traps. Skinner (1983) also recorded this bug migrating into apple orchards in late summer.

In 1984, when bug migration from WM110 was considerably less than in 1983 (figs.181 -183) a different picture emerged. Total numbers of predators recorded were lower than in 1983, mainly due to the absence of B.angulatus. In 1983 a total of 1174 adult capsids was recorded upon the edge traps; in 1984 this figure was 156. The average number of predators per trap in 1984 was 194 on the edge traps and 128 on the orchard traps. Thus despite the lower numbers, edge traps still caught more predators than did the orchard traps ($t=5.6$, $p<0.001$). In 1984, the percentage catch of B.angulatus on the edge traps was 13.4%, almost identical to the 13.5% recorded in the orchard. The commonest predator in 1984 in percentage terms was M.chlorizans, comprising 63% on the edge traps and 62% in the orchard. This was not due to it being commoner than in 1983 however, for there was no difference in the average number of this bug caught per trap in 1983 and 1984 ($t=0.37$, $p>0.05$). It simply appeared to be commoner due to the lack of B.angulatus. Therefore, in a year when migration from a windbreak is low, the orchard edge traps do not catch a higher percentage of capsid adults. Only when capsids leave alder in large numbers does this occur, thus strongly supporting the suggestion that B.angulatus leaves alder windbreaks and colonizes apple orchards in late summer.

6.5. DISCUSSION

The results presented here indicate that P.alni represents an acceptable food supply for B.angulatus. Capsids reared on this aphid at 15°C were similar in size to those reared at 14°C by Glen (1973) using lime aphids as food. Overall, the dry weight of aphids consumed during development was 1.324 mg. in Glen's study and in the current work this figure was similar but lower (1.279 mg). The growth efficiency of both male and female capsids was higher when reared on P.alni compared to E.tiliae and thus it may be that the alder aphid provides a better quality food supply for B.angulatus than does the lime aphid.

The food consumption of B.angulatus nymphs increases at an increasing rate as they develop. In the fifth instar the consumption was 55% of the total consumed by the nymphs. This is similar to the figure of 50% reported by Glen (1973) and for other predatory Heteroptera, such as A.nemorum and A.confusus (Russel, 1970). As the growth efficiency of later instars is lower than that of young bugs it is to be expected that their prey consumption would be higher, because they are less efficient at utilizing the prey captured. At maturity, males are significantly lighter than females. Smith, B.C. (1966) working with various coccinellid species considered that because males were lighter at maturity they may be more able to survive when prey was scarce, thereby causing an increase in the proportion of males in the population. However, B.angulatus males are less efficient in using food than females. In addition, there were always aphids present when capsids were in the fifth instar in the field, thus this situation is unlikely to occur.

In this study the effects of partial starvation of capsid nymphs was not investigated, as this situation is unlikely to occur in the field. Glen (1973 showed that if capsids were short of food from the third instar onwards

then adults were lighter at maturity. Of the alternative foods available, only parasitised aphid mummies allowed development to proceed normally. Honeydew provided a food source for a time; survival could be prolonged on this but development could not continue. On alder, the synchrony of of aphid populations and the capsid development mean that it is unlikely that the later instars go short of food. In years such as 1984 on WM110 when initial aphid numbers were low, first instar capsids may have gone short of food and some starvation may have occurred, indicated by the relatively high values of k_1 in that year. B.angulatus can compensate for food shortage in early instars by converting food into body tissue with a greater efficiency. It is therefore likely that B.angulatus can experience a certain amount of food shortage in early instars, without detriment to the final adult weight. In years when aphid populations peaked early, survival may have been aided by feeding on mummies or the copious amounts of honeydew remaining after the high aphid numbers. Another possibility not considered by Glen is cannabalism. This was considered to represent a significant mortality by Collyer (1964) when the food supply was limited. Once capsids reach the fifth instar they would be large enough to capture adult leafhoppers such as E.alneti, K.smaragdula or T.jucunda. Although rarely recorded on the windbreaks in this study they may have aided capsid survival if aphid numbers became very low. The only other possible prey recorded on the alder were young larvae of the Purple Thorn moth, Selenia tetralunaria Hufnagel found during August.

Although only a limited amound of data is available, the life table analyses of B.angulatus populations suggest that the key mortality factor is the emigration of females from the windbreak and the consequent loss of eggs. The substantial emigration in years when aphid numbers peaked early mirrors that recorded by Glen and Barlow (1980) from lime trees. Muir (1966b) and Solomon (1975b) also found that B.angulatus has a marked tendency to disperse by flight. Waloff and Bakker (1963) studying five mirid species

on broom, Sarothamnus scoparius (L) Wimmer also noted dispersal by flight. In that case the bugs migrated for a short time only, before laying eggs, although trivial flights or 'flitting' occurred throughout adult life. Unless aphids became virtually absent upon the leaves, some female bugs always remained upon the windbreaks. Males always flew from the alder and even on occasions when migration was extensive, more males flew than females. A greater tendency to disperse among males than with females was also noted for this species (Muir,1957), for the mirids on broom (Waloff and Bakker, 1963) and appears to be generally true for most of the Heteroptera (Southwood, 1960). The fact that a number of females always remained is important as it ensures a supply of eggs for the following season. Glen and Barlow (1980) found that the flight activity of female B.angulatus reaches a peak 16-25 days after the adult moult, subsequently declining sharply as the ovaries mature. Flight activity of males continues to be high throughout adult life. Thus if there are sufficient aphids present upon the leaves, female B.angulatus are less likely to leave the windbreak. As they age they are less likely to fly although aphid numbers may decrease during this time. Glen (1973) reported that adult female capsids consumed between 0.334 mg and 0.52 mg of lime aphids per day, the consumption increasing with the age of the bug. Although not investigated in this study, this would represent 1-2 adults of P.alni per day in late summer/early autumn. Leaf samples indicate that at worst a capsid would have to search about 100 leaves per day to find sufficient food. Using the figures reported by Glen (1975) for the average time spent searching by an adult female this would amount to 11.3 hours per day spent searching for food. This figure is likely to be somewhat inaccurate, having used the average area covered per minute at 18^{o}C. However, it assumes that the only potential prey likely to be encountered are aphids and this may not be true. Despite appearing an inordinate length of time to be searching for food, capsids remain on the alder where there is at least some food, rather than emigrating and risk not finding any. The result is that capsid

numbers increased on six out of eight windbreak situations studied and only showed a decrease when aphids became absent. When capsids suffered a bad year it appeared that it would take only 5 years for numbers to recover, although this figure needs verification, through further years of field observations. This is in contrast to the 20 years reported by Glen and Barlow (1980) for the bug on lime trees. The reasons for this may be as follows. As previously stated, the tendency for some females to remain upon the alder results in eggs being laid and if conditions are at all favourable the numbers will increase from one year to the next. In Glen and Barlow's study the lime trees were in a single row and there was no potential source of immigrants in the direction of the prevailing wind, which would have increased numbers upon the trees. Although a windbreak is also a line of trees, it is double and thus bug (and aphid) numbers may not be similar on each face. Migration may therefore occur through the windbreak. At East Malling there are numerous potential sources of emigrating capsids in the form of other alder windbreaks and it is therefore likely that immigration to each windbreak occurs. A third possibility is the extent of parasitism recorded in B.angulatus populations at East Malling. Very few parasitized individuals were found in the current study and a similar result was recorded by Collyer (1964)also working at East Malling. In contrast, Glen (1977b) recorded a level of parasitism as high as 80% on lime trees in Glasgow. Therefore parasitism, by reducing the numbers of emerging adults could have reduced the potential number of eggs laid and thus the capsid number in the following year. At East Malling where B.angulatus is relatively free from parasitism such reductions did not occur and capsid numbers are more likely to increase each year. Parasitized B.angulatus consume twice as much food in the fifth instar as do unparasitized individuals (Glen,1977b). In the same paper it is stated that on lime the prey density is such that this can occur. However, on apple, where capsids are smaller (indicating that the food supply is less plentiful) parasitism rarely occurs as the ecological conditions necessary

(plenty of prey when the capsids are fifth instar) are not satisfied. It is interesting to note that on alder, where prey is plentiful the conditions for parasitism would appear to be satisfied and clearly this does not occur. Alder windbreaks are a relatively recent (within the last 15 years) addition to orchards and it may be that the parasites do not occur at East Malling due to there being no suitable conditions in the past or that this is a food supply as yet unexploited by the parasite.

In this work it appears that B.angulatus failed to regulate P.alni populations on alder. It is likely that it has an effect upon late summer numbers although in no case was a recovery of aphid numbers prevented by the bug. This is important if B.angulatus is to play a useful part in an integrated programme of pest control in orchards. The fact that some bugs always migrate means that there will always be some colonization of orchards in summer. The fact that these are mostly males means that few eggs will be laid in the orchard. However, this also means that eggs are laid on the windbreak ensuring a supply of capsids the following year. When aphid numbers are low, bugs do not prevent recovery of the aphids therefore ensuring a food supply for the following year's capsid nymphs. In years when the autumnal populations of aphids are relatively high, more capsid eggs are laid, resulting in more nymphs the following year. In the 'normal' course of events, the subsequently high spring aphid numbers would result in an early peaking and declining aphid population and as a consequence a large migration in which most of the bugs migrate. Such an event occurred on LF125 in 1983. If pruning occurs after the population has peaked aphid numbers are reduced still further and virtually all the capsids migrate. Such a situation occurred on WM110 sections 1 and 3 in 1983. However, if pruning occurs early relative to the aphid population peak, then the numbers are reduced and subsequent autumn numbers are higher than on unpruned sections (table 34). In this case more bugs remain upon the windbreak and thus the numbers increase, whilst there is still a migration.

Such an event occurred on WM110 sections 1 and 3 in 1984. The situation on alder windbreaks is thus very different from that described by Glen and Barlow (1980) on lime. On windbreaks the migration of the bug may be affected by cultural control of its prey's host plant. The fact that windbreaks support a viable bug population every year shows that B.angulatus can withstand pruning practices and in some years may benefit from them. The planting of alder, especially A.glutinosa, has therefore helped to create a considerable reservoir of B.angulatus close to many orchards (Solomon, 1981).

The colonization of an orchard by B.angulatus has been reported by Solomon (1975b). In that study, B.angulatus colonized selectively sprayed orchards at a rate of four per tree in response to P.ulmi densities as low as two per leaf. The source of the capsids was nearby alder and the disappearance of the adults from alder coincided with their appearance in the orchard and in suction trap catches. In another study (Solomon,1975a) when alder was absent, P.ulmi densities exceeded ten per leaf but the number of colonizing B.angulatus was only one per tree. In this study the sticky trap catches at the orchard edge showed the colonization of the orchard by B.angulatus adults as they left the alder windbreak. These dispersed amongst the trees and the traps within the orchard showed greater numbers of capsids flying than in a year when migration was less. It is extremely unlikely that the orchard was the source of B.angulatus in this study as it received a broad spectrum spray programme.

The emigration of B.angulatus has been shown to be closely related to the changes in abundance of its main food on alder, P.alni. However the importance of other possible prey species in the diet of this bug have not been assessed. In particular the role of the leafhopper species should be investigated. Examination of the gut contents of B.angulatus by electrophoresis such as the method of Murray and Solomon (1978) would allow

the rapid determination of prey species and whether leafhoppers are important.

Few other predators present on alder are likely to be important colonizers of orchards. Coccinellids were uncommon on all windbreaks sampled. Anthocorids, mainly A.nemorum were fairly common on A.glutinosa but appeared to show little migratory activity. Anthocorids have been shown to be of value in an integrated control system against hop aphids (Aveling,1981) but in that study there was little evidence to suggest migration from nearby non-crop habitats such as hedges. O.marginalis appeared as adults earlier in the season on alder and also exhibited migratory activity in a similar manner to B.angulatus. All migration, however, occurred when aphid numbers were increasing or high, thus the stimulus for migration in this species would make an interesting and important comparison with B.angulatus. Its numbers were always lower on alder than B.angulatus and a detailed examination of its biology may help to explain why this is so and whether it could exist on alder in greater numbers. The potential of this bug in integrated control may be substantial. It is a voracious predator of aphids and spider mites (Alford, 1984) and by migration to apple earlier in the year than B.angulatus could provide a continuous supply of predators immigrating into orchards from June until September.

Large numbers of M.chlorizans immigrated into the orchard, although no specimens of this bug were ever found upon any of the windbreaks sampled. Skinner (1983) also found M.chlorizans immigrating into orchards in large numbers, but found very few nymphs present on the apple trees. Thus even in unsprayed orchards M.chlorizans was not a large constituent of the orchard fauna. The question naturally arises as to the origin of these bugs. Southwood and Leston (1959) state that it is especially common on hazel, a view supported by Alford (1984). An investigation into its biology may reveal the origin of this bug and its potential as a colonizing predator in apple orchards. Why it should colonize orchards and apparently

ignore nearby alder, which in this study at least provided a greater food supply, also needs to be answered. The possibilities of introducing it on to alder may then also be considered.

Chapter 7 GENERAL DISCUSSION

The specific points raised by this study have been discussed in the appropriate sections but a consideration of the overall ecology of P.alni and its role in integrated pest control in orchards remain.

The term 'ecology' has been used here in a manner similar to Dixon (1985a) in that it includes aspects of the biology of the aphid, necessary for an understanding of population change.

The population dynamics of P.alni have been studied at Lyne and East Malling. Differences in abundance were noticeable between sites and influenced changes in the populations. Stroyan's (1977) description of this aphid as 'local but very widespread, rarely very abundant' has been found to be apt during this study. P.alni shows a distinct preference for young trees or bushes such as those sampled at Lyne. In that locality aphids were only very occasionally found on the mature trees present. Mature alder was examined near East Malling in an area where the aphid was obviously common. The mature trees had very few aphids whereas sapling trees planted 100m distant carried large numbers. The windbreaks at East Malling are pruned annually and consequently produce a large crop of growth each year, thus these trees are similar to young saplings which are actively growing. The aphid appears to favour these conditions and was abundant every year on A.glutinosa. This preference may help to explain why during 1982 sampling of mature A.glutinosa at Alice Holt, Farnham, Surrey (Forestry Commission Research Station), Silwood Park, Berkshire (Imperial College),Egham,Surrey and Windsor, Berks produced very few aphids.

P.alni was considerably rarer at Lyne than East Malling and indeed, less numerous than other holocyclic species whose populations have been studied

in detail. Numbers of D.platanoidis in spring between 1961 and 1970 were lowest in 1962 at two per leaf (Dixon 1970a). The highest recorded density at Lyne in spring was one per ten leaves or 0.1 leaf^{-1}. Maximum numbers of E.tiliae reach about 10,000m^{-2} (Barlow and Dixon, 1980). The maximum number of P.alni recorded at Lyne was 600m^{-2}. Figures of abundance for P.alni at East Malling were very similar to those of D.platanoidis and E.tiliae. Although the time scale of this study has been shorter than that of D.platanoidis and E.tiliae, certain population trends have emerged. The populations at East Malling, when pruning or spraying did not intervene, tended to show a cycle alternating between high and low numbers. A relatively high initial number of fundatrices in spring resulted in a high population which reached its peak in mid July. Numbers declined sharply and few oviparae were produced in autumn. When fundatrices were scarce the population peaks occurred in early August and were lower than those previously described. Following these low peaks, oviparae were relatively common thus completing the two year cycle.

Populations at Lyne also appeared to fluctuate in a two year cycle, but in a different fashion to East Malling. At Lyne, low fundatrix numbers produced late peaking populations and high numbers, early populations. However, in contrast to East Malling and also to E.tiliae (Dixon,1971c) the late peaking populations were higher than the early peaking examples. It is likely that this was due to the scarcity of aphids and that alate forms which are produced due to crowding did not appear until late in the season.

In P.alni a combination of factors act to influence the population changes. Crowding individuals results in the production of winged forms, both mother and offspring being responsive to crowding. As numbers on the leaves increase more alatae appear in the population. The combination of decreasing food quality, increased crowding and higher temperatures, all of which occur

during June, result in the production of successively smaller and less fecund aphids. The recruitment begins to fall and the population collapses when emigration of alatae exceeds recruitment. This situation occurred at Lyne and East Malling but alatae were produced later at Lyne because original numbers were so low as to provide little or no crowding stimuli. Late numbers attained were therefore higher, due to the reproduction of the apterous second and third generations. At Lyne, alatae appeared in the third and fourth generations; at East Malling they were produced in the second and third.

The question arises as to why populations were so low at Lyne and remained so. Predators, parasites and diseases were not as common at Lyne as at East Malling and the food quality as measured by foliar soluble nitrogen was similar. The populations appeared to be regulated by the same constraints in each site and it may be that extremely low populations remain that way only increasing if some or all of these constraints are removed. The effects of weather on field numbers can never be removed. Dixon (1979) states that wind is an important mortality factor affecting both the lime and sycamore aphids. It may be possible that weather conditions were more severe at Lyne than at East Malling, but this is unclear. Certainly very small populations risk extinction and this occurred on two occasions. Populations on these branches were then initiated by the arrival of alatae.

The aphid populations at East Malling were considerably affected by annual pruning of the windbreak. Bug populations were not seriously affected. This may be due to the fact that B.angulatus, a highly mobile predator, is more able to maintain its position on the windbreak than the smaller, relatively sedentary aphid. Bugs returning to the windbreak via tree trunks were not examined but a banding of 'Oecotak' around each trunk may show if this resulted in a change in numbers.

Capsid numbers and migration were indirectly affected by pruning by its

effect on aphid numbers. Early pruning of an aphid population before it peaked reduced the maximum level attained and final ovipara numbers were higher relative to the unpruned section. Pruning after the population had peaked simply reduced the declining numbers still further and oviparae were fewer than the controls. Once the crowding stimulus is not experienced by alatae the tendency to fly is lessened. Thus more alatae remain on early pruned sections resulting in more late summer generations of apterae. Due to the improved food quality and lower temperatures during September, these are large and highly fecund, giving rise to many sexuales. Capsid migration from the windbreak reported by Solomon (1975a,b) is closely linked to changes in abundance of its main prey, P.alni. If aphids are numerous during August, male capsids migrate into the orchard but females tend to remain on the windbreak. If, however, aphids become extremely scarce, for example by late pruning an already-peaked population, then both sexes of the bug migrate, resulting in a substantial loss of females and a decrease in capsid numbers the following year. In unsprayed orchards, B.angulatus can prevent the fruit tree red spider mite from becoming abundant (Collyer, 1953). However, this bug cannot survive in the modern commercial orchard receiving a programme of broad-spectrum pesticides. When it is possible to obtain sufficiently selective insecticides which kill a few key pests then the colonization of orchards by predators where none existed will become important. Such colonization will aid in control and relieve the selection pressure for resistance to chemicals.

From these results it would appear that it would be advantageous to prune a windbreak before or near the peak time of aphid numbers. This would result in an increased aphid population in autumn, resulting in a food supply for the adult capsids at the important time of oviposition in late August. Capsid numbers would therefore increase the following year due to the success of egg laying. Aphid numbers would be high and thus provide all emerging capsid nymphs in June with a plentiful food supply. By

pruning early, aphids would be numerous during August and mainly male capsids would migrate. Adult males have voracious appetites (Collyer,1952; Glen,1973) and would therefore aid in the control of P.ulmi and other orchard pests. The detailed biology of P.alni described in this work should enable a simulation model of alder aphid populations to be produced. Similar models have been produced for D.platanoidis (Chambers,1979) and E.tiliae (Barlow and Dixon,1980). Such a model of P.alni will need to incorporate not only the biology of the aphid and the capsid but also environmental variables such as weather conditions and the cultural control of the alder host. The production of a model such as this would fully test our understanding of the population dynamics of this aphid. By simple sampling, information may be gained in each year to predict the time of pruning most advantageous to the aphid and the bug. Careful considerations of a management system such as this need to be taken so that the colonization of orchards by the predator is reliable and occurs at a useful time. If aphid populations become extremely low, many bugs will migrate. This may be desirable in that particular year but could have disastrous effects in later years in terms of reduced capsid numbers. Results here suggest that after a 'bad' year it would take B.angulatus four years to recover its numbers.

The data presented here suggest that A.glutinosa can provide a reservoir of capsid bugs close to orchards. However, it is not known to what level B.angulatus could exist on alder without affecting numbers of its prey. Using the model of Barlow and Dixon (1980), Glen and Barlow (1980) investigated the effects of changing aphid and capsid densities on the rate of increase of the capsids from year to year. They found that at densities of capsids ten times the average the rate of increase was inevitably less than one and initially low aphid populations could be eliminated. Their conclusion was that B.angulatus is incapable of existing on lime above the observed maximum because of a potentially regulating interaction with its

prey. From field observations at East Malling it is impossible to say whether the levels of B.angulatus recorded upon the windbreaks were the maximum possible. Pruning each year has such an effect on the aphid and bug numbers that the natural cycles may be obscured. Thus a potentially dangerous situation to the bug of loss of food in August or to the aphid of high bug numbers in August can be altered completely by the timing of pruning. The model will hopefully tell us the levels at which B.angulatus can exist on alder without detriment to itself or the aphid. However as field observations showed that on some occasions there were 10 adult capsids found to every aphid and still the bug numbers increased the following year it appears that capsid levels higher than those generally recorded could exist. A ratio of ten bugs to one aphid is extremely unlikely and suggests that alternative sources of food for the bug should be investigated. It may reflect a chance occurrence in the sampling technique but ratios of six to one were frequently found, suggesting that perhaps the bug is extremely efficient at searching for and capturing P.alni.

It certainly appears that B.angulatus developing on A.glutinosa feeding on P.alni has great potential in integrated orchard pest control, if the system is managed carefully. P.alni is somewhat unusual amongst the tree dwelling Callaphididae in exhibiting polymorphism. Sixty-five per cent of this family are winged in all generations except the oviparae (Dixon,1984) and it is suggested that the polymorphism exhibited by many tree dwelling aphids may be a consequence of their clonal structure and division of labour between morphs. This is in contrast to the proposal of Waloff (1983) that tree dwelling insects are more likely to be winged than those living on herbaceous plants. P.alni through its polymorphism appears to exploit its alder host very efficiently. The possession of apterous adults means that reproduction can occur at a greater rate than if these were winged. The production of winged individuals occurs at a time when the host plant is least suitable and migration may occur to colonize a new alder host.

The food quality of alder does not deteriorate to such an extent as other British trees and this has been attributed to its nitrogen fixing ability (Wittwer and Immel,1980). If uncrowded, P.alni can remain on alder reproducing throughout the year, steadily, unlike D.platanoidis (Dixon 1963). When the harsh conditions in summer are relieved i.e. the population has collapsed and crowding is less severe, the alatae present do not fly but remain and produce apterous offspring successive generations of which are larger and more fecund, thereby enabling the population to increase again in autumn, in contrast to E.tiliae which cannot recover from the harsh conditions of summer, due to the poor quality of the aphids present (Dixon,1971c). In these respects P.alni can therefore respond rapidly to the changes in its host plant created by cultural control i.e. pruning. The changes are brought about by an artificial reduction in crowding which means that the aphid can exploit its host again. Pruning early is therefore to the aphid's advantage. Pruning late is to its disadvantage as numbers can be virtually eliminated and no subsequent recovery occurs. An interesting example of the pruning of a host being of advantage to an insect was provided by Webb and Moran (1978). In that case numbers of the psyllid Acizzia russellae Webb and Moran were increased ten times by pruning its host tree A.karoo. The population levels were attained on regenerative foliage which was high in amino-nitrogen compared to older leaf tissue.

Pruning alder early is of advantage to the bug as its food supply is enhanced. Therefore the cultural control of alder is an important part of any integrated control programme.

Throughout this discussion attention has been fixed upon windbreaks of A.glutinosa. Current planting practices of windbreaks at East Malling involve replacing many A.glutinosa windbreaks with A.cordata (Way,1984). A.cordata performs better on dry soils where the growth of A.glutinosa may be uneven. A.cordata has the disadvantage of leafing very late in

the year and the results of this study show that it does not carry a complete crop of foliage until June and is therefore not effective at the important blossom time. A deciduous conifer, Larix leptolepis Gordon, the Japanese larch, is currently undergoing trials as it leafs earlier than A.cordata and withstands pruning well (Way,1984). This study suggests that A.hybrida may be a very worthwhile candidate for windbreak trials. Observations at Lyne have shown that buds of A.hybrida burst very early in the year and that there is a good crop of leaves available during April; considerably earlier than A.cordata. One of the advantages of A.cordata, namely retaining a full canopy of leaves well beyond the apple harvest (Baxter, 1979) is also possessed by A.hybrida. From the point of view of integrated control, A.cordata is potentially of little use. Few aphids were ever found upon it and as a consequence of the scarcity of its prey, B.angulatus was rarely recorded on this species. B.angulatus is also absent from the windbreaks at Long Ashton Research Station, Bristol (D.M.Glen,pers.comm.) where these are also composed of A.cordata. An important consideration when choosing a windbreak is whether it harbours pests or pathogens of the fruit crops which it protects (Baxter,1979; Solomon,1981). Sampling of A.hybrida at Lyne revealed no insects which are regarded as orchard pests (Alford,1984). Rigorous trials of this species at East Malling would reveal whether or not A.hybrida would act as a reservoir of pests as well as predators.

This study has shown that A.hybrida supports populations of P.alni very similar to those on A.glutinosa. The early bursting habit of A.hybrida did not appear to put fundatrices upon it to any disadvantage and populations increased in a similar manner on both species. It is not known how well this species would respond to annual pruning but it is likely that it would withstand this well. As a result of being a hybrid it appears to possess 'hybrid vigour' and this is manifested in such things as cone and leaf size (both larger than A.glutinosa or A.incana)

growth (faster and more in a season than its parents) and the bursting of buds well before its parents. It is therefore likely that regrowth would occur after pruning and with the increased leaf size, form a dense windbreak. It is not known whether A.hybrida would grow well on dry soils but one of its parents does (A.incana, Baxter,1979) and combined with hybrid vigour this is a likely possibility.

B.angulatus was found upon A.hybrida at Lyne and therefore it is likely that windbreaks of this species would form reservoirs of this predator unlike A.cordata. By planting A.cordata the possibilities of orchard colonization by useful predators (Solomon 1975a,b) is eliminated and control in orchards must be by chemical means with the associated problems of resistance becoming more apparent. Many problems with insecticide resistance of fruit tree red spider mite have arisen in the past (Cranham, 1978). This study suggests that windbreaks of hybrid alder will combine the physical advantages of A.cordata with the potential of integrated control inherent in A.glutinosa.

Predators other than B.angulatus may also play a role in integrated pest control. Anthocorids especially A.nemoralis may be useful in controlling the pear sucker, P.pyricola (Solomon,Cranham, Easterbrook and Souter, 1979) and chemicals such as amitraz ('Mitac') and Avermectin exert some control over the sucker whilst being harmless to A.nemoralis (Campbell et al, 1984). Anthocorids were found on the windbreaks and also at Lyne, although they were never as numerous as B.angulatus. Their capacity for increase is greater than B.angulatus, for example A.nemorum has two or even three generations during the summer (Southwood and Leston,1959). Anthocorids do not appear to colonize hop gardens from nearby hedgerows (Aveling,1981; Campbell, 1984) but migrate over relatively large distances. However, the formation of a reservoir of these bugs on alder may be an important part of an integrated control programme. Such a programme could not exist

if A.cordata is planted but could do so with A.hybrida.

Two remaining possibilities suggested by this study are the mirids O.marginalis and M.chlorizans. It has been reported that colonizers such as B.angulatus may arrive in the orchard too late in summer to prevent populations of P.ulmi reaching high levels (Solomon,1975a). Late colonization would result when aphid numbers on the windbreak are relatively high during August. O.marginalis appears to migrate earlier in the year and an investigation of its biology on alder and possibilities of use in an integrated control programme would be useful.

Although M.chlorizans was noted by Skinner (1983) and in this study to immigrate into orchards in large numbers its origin is still unclear. Solomon and Fitzgerald (1984) using electrophoretic analysis of gut contents found that this bug feeds on Psylla mali Schmidberger, the apple sucker, a serious pest on unsprayed trees (Alford 1984). An investigation into its biology and sources of colonization would establish whether it may also be useful in integrated control.

The phytoseiid mite Typhlodromus pyri Scheuten has also been shown to colonize orchards (Solomon 1975b). Little is known of the way it moves into orchards and during this study no specimens were found on any alder species. Therefore it is unlikely that colonization occurs from the alder and its value as a predator may lie in mass introduction (Solomon and Fitzgerald, 1984b).

In conclusion, this study has focussed on the ecology of P.alni. This aphid is abundant on windbreaks of A.glutinosa which have become a feature of orchards in the past 15 years. A detailed examination of its biology has helped to explain changes in its abundance within and between years. Also present on A.glutinosa are populations of B.angulatus and changes in

abundance of this capsid reflect those of its aphid prey. Annual summer pruning has a great effect on aphid and capsid numbers. It should be possible to predict changes in abundance of predators and prey and to manage these successfully in an integrated system of orchard pest control. The development of selective pesticides, the re-examination of windbreak species planted and the possibilities of other predators may all have parts to play in future successful orchard pest management.

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APPENDIX 1.1 FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1982

		B R A N C H 1 % of Leaves with Aphids of Number:						
Date	0	1	2	3	4	5	6	>6
April 15	100	0	0	0	0	0	0	0
21	98	2	0	0	0	0	0	0
28	97	3	0	0	0	0	0	0
May 5	95	3	2	0	0	0	0	0
12	89	6	5	0	0	0	0	0
19	82	8	7	1	0.5	0	0.5	1
26	88	5	2	2	1	1	0	1
June 2	85	8	4	1	0.25	0.5	0.25	1
9	82	11	4	1.75	0.25	0.25	0.5	0.5
16	79.5	12.5	4	2	0.5	0.25	0.25	1
23	84	12	2.5	0.25	0.25	1	0	0
30	90	6.5	3	0.5	0	0	0	0
July 7	94	5	1	0	0	0	0	0
14	96	4	0	0	0	0	0	0
21	96	3.5	0.5	0	0	0	0	0
28	97.5	2	0	0.5	0	0	0	0
Aug 4	99	1	0	0	0	0	0	0
11	97	2	0.5	0	0	0.5	0	0
18	96	3	1	0	0	0	0	0
25	97	3	0	0	0	0	0	0
Sept 1	97	2	1	0	0	0	0	0
8	96	3	0	1	0	0	0	0
15	97	2	0	1	0	0	0	0
22	98	1.5	0.5	0	0	0	0	0
29	99	1	0	0	0	0	0	0
Oct 6	99	1	0	0	0	0	0	0
13	99	1	0	0	0	0	0	0
20	99	1	0	0	0	0	0	0
27	99	1	0	0	0	0	0	0
Nov 3	99	1	0	0	0	0	0	0
10	99	1	0	0	0	0	0	0
17	99	1	0	0	0	0	0	0

APPENDIX 1.1 cont. FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1982

		B R A N C H 2 % of Leaves with Aphids of Number:						
Date	0	1	2	3	4	5	6	>6
April 15	0	0	0	0	0	0	0	0
21	99	1	0	0	0	0	0	0
28	99	1	0	0	0	0	0	0
May 5	98	2	0	0	0	0	0	0
12	95	3	1.5	0.25	0.25	0	0	0
19	91.5	5.5	2	0.25	0.25	0.25	0	0.25
26	88	7	3	1	0.25	0.25	0	0.5
June 2	88.5	8	2	0.5	0.25	0.5	0	0.25
9	87	9	2	0	0.5	0.5	0	1
16	84	11	2	1	1	0.5	0	0.5
23	87	8	2.5	1	0.5	0.5	0	0.5
30	89	9	0.75	0.5	0.25	0.25	0.25	0
July 7	96	3	1	0	0	0	0	0
14	95	4	0	0	1	0	0	0
21	97	3	0	0	0	0	0	0
28	98.5	1	0.25	0	0	0	0	0.25
Aug 4	98.5	1.25	0	0.25	0	0	0	0
11	98	1.75	0	0.25	0	0	0	0
18	97	2	0.5	0	0	0	0	0.5
25	96	3.25	0.5	0	0	0.25	0	0
Sept 1	96.75	3	0.25	0	0	0	0	0
8	97	2.75	0.25	0	0	0	0	0
15	98.25	1.5	0.25	0	0	0	0	0
22	99	1	0	0	0	0	0	0
29	99	1	0	0	0	0	0	0
Oct 6	99	0.5	0	0	0	0.5	0	0
13	99	1	0	0	0	0	0	0
20	99	1	0	0	0	0	0	0
27	99	1	0	0	0	0	0	0
Nov 3	99	1	0	0	0	0	0	0
10	99	1	0	0	0	0	0	0
17	99	1	0	0	0	0	0	0

APPENDIX 1.2 FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1982

B R A N C H 3
% of Leaves with Aphids of Number:

Date		0	1	2	3	4	5	6	>6
April	15	100	0	0	0	0	0	0	0
	21	93	6	1	0	0	0	0	0
	28	93	6	1	0	0	0	0	0
May	5	94	5	1	0	0	0	0	0
	12	95	3	0	0	0	0	0	0
	19	78	15	2	1	1	1	1	1
	26	70	16	5	3	1	1	1	3
June	2	70	14	5	4	1	1	1	4
	9	70	14	7	2	2	1	1	3
	16	58	24	6	5	2	1	1	3
	23	69	19	6	2	1	0	1	1
	30	84	12	3	0.5	0.5	0	0	0
July	7	91	8	1	0	0	0	0	0
	14	93.5	6	0.5	0	0	0	0	0
	21	96	4	0	0	0	0	0	0
	28	99	1	0	0	0	0	0	0
Aug	4	98	1.5	0	0.5	0	0	0	0
	11	96	4	0	0	0	0	0	0
	18	95	4	1	0	0	0	0	0
	25	96	4	0	0	0	0	0	0
Sept	1	96	4	0	0	0	0	0	0
	8	98	2	0	0	0	0	0	0
	15	99	1	0	0	0	0	0	0
	22	99	1	0	0	0	0	0	0
	29	99	1	0	0	0	0	0	0
Oct	6	97	3	0	0	0	0	0	0
	13	98	2	0	0	0	0	0	0
	20	98	2	0	0	0	0	0	0
	27	98	2	0	0	0	0	0	0
Nov	3	98	2	0	0	0	0	0	0
	10	98	2	0	0	0	0	0	0
	17	100	0	0	0	0	0	0	0

APPENDIX 1.2 cont. FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1982

B R A N C H 4

% of Leaves with Aphids of Number:

Date		0	1	2	3	4	5	6	>6
April	15	100	0	0	0	0	0	0	0
	21	99	1	0	0	0	0	0	0
	28	99	0.5	0.5	0	0	0	0	0
May	5	98	2	0	0	0	0	0	0
	12	98	1	0	0	0	0	0	0
	19	91	6	1	1	0	0	0	0
	26	93	5	1	0.5	0.5	0	0	0
June	2	91	7	1	0.25	0.25	0.25	0	0.25
	9	73	15	6	2	1	1	1	1
	16	76	16	5	2	1	0	0	0
	23	81	14	3	1	1	0	0	0
	30	87	9	2	1	1	0	0	0
July	7	95	5	0	0	0	0	0	0
	14	93	7	0	0	0	0	0	0
	21	97	3	0	0	0	0	0	0
	28	97	3	0	0	0	0	0	0
Aug	4	97	3	0	0	0	0	0	0
	11	98	2	0	0	0	0	0	0
	18	98	2	0	0	0	0	0	0
	25	98	2	0	0	0	0	0	0
Sept	1	99	1	0	0	0	0	0	0
	8	100	0	0	0	0	0	0	0
	15	100	0	0	0	0	0	0	0
	22	100	0	0	0	0	0	0	0
	29	100	0	0	0	0	0	0	0
Oct	6	99	1	0	0	0	0	0	0
	13	100	0	0	0	0	0	0	0
	20	100	0	0	0	0	0	0	0
	27	100	0	0	0	0	0	0	0
Nov	3	100	0	0	0	0	0	0	0
	10	100	0	0	0	0	0	0	0
	17	100	0	0	0	0	0	0	0

APPENDIX 1.3 FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1982

		THE BUSH						
		% of Leaves with Aphids of Number:						
Date	0	1	2	3	4	5	6	>6
						0	0	0
April 15	100	0	0	0	0	0	0	0
21	99	1	0	0	0	0	0	0
28	98	1	1	0	0	0	0	0
May 5	95	2.75	1	1	0.25	0	0	0
12	93	4	1	1	0.5	0.25	0.25	0
19	89	5	2	2	0.5	0.25	0.25	1
26	87	7	3	1	0.5	0.25	0.25	1
June 2	86	6	3	2	1	0.5	0.5	1
9	81	9	5	2	1	0.5	0.5	1
16	76	14	4	2	1	1	1	1
23	80	10.5	3.5	2	1	0.5	0.5	2
30	83	10	3	1	1	0.5	0.5	1
July 7	87	9	1	1	0.5	0	0.5	1
14	92	5.75	1	0.5	0.5	0	0	0.25
21	96.75	2.5	0.5	0	0.25	0	0	0
28	98.75	1	0.25	0	0	0	0	0
Aug 4	99.25	0.5	0.25	0	0	0	0	0
11	99	0.5	0.125	0	0.25	0	0.125	0
18	96.75	2.75	0.25	0.25	0	0	0	0
25	97.5	2.25	0.25	0	0	0	0	0
Sept 1	98	1.75	0.25	0	0	0	0	0
8	99	1	0	0	0	0	0	0
15	99.5	0.5	0	0	0	0	0	0
22	99.5	0.5	0	0	0	0	0	0
29	99.5	0.5	0	0	0	0	0	0
Oct 6	99.5	0.5	0	0	0	0	0	0
13	99.5	0.5	0	0	0	0	0	0
20	99.5	0.5	0	0	0	0	0	0
27	99.5	0.5	0	0	0	0	0	0
Nov 3	99.5	0.5	0	0	0	0	0	0
10	99.5	0.5	0	0	0	0	0	0
17	99.5	0.5	0	0	0	0	0	0

APPENDIX 1.4 FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1983

		B R A N C H 1 % of Leaves with Aphids of Number:						
Date	0	1	2	3	4	5	6	>6
April 20	100	0	0	0	0	0	0	0
27	100	0	0	0	0	0	0	0
May 4	100	0	0	0	0	0	0	0
11	100	0	0	0	0	0	0	0
18	100	0	0	0	0	0	0	0
25	100	0	0	0	0	0	0	0
June 8	99.5	0.25	0.25	0	0	0	0	0
15	94	4	1	1	0	0	0	0
22	89	5	3	1	0	1	0	1
29	87	5	2	1	1	1	1	2
July 5	85	5	4	1	0.5	1	0.5	3
13	54	14	8	8	3	3	3	7
20	65	17	6	4	2	1	1	4
27	82	10	5	1	1	0.5	0	0.5
Aug 3	81	12	3	2.5	1	0	0.5	0
10	89	9	1	1	0	0	0	0
17	95	4.5	0.25	0.25	0	0	0	0
24	95	4	1	0	0	0	0	0
31	92	5	1.5	1.5	0	0	0	0
Sept 7	94	4	1	1	0	0	0	0
14	95	4	1	0	0	0	0	0
21	97	3	0	0	0	0	0	0
28	97.5	2.5	0	0	0	0	0	0
Oct 5	99	1	0	0	0	0	0	0
12	99	1	0	0	0	0	0	0
19	99	1	0	0	0	0	0	0
26	99.5	0.5	0	0	0	0	0	0
Nov 2	99.5	0.5	0	0	0	0	0	0
9	99.5	0.5	0	0	0	0	0	0
16	99.5	0.5	0	0	0	0	0	0

APPENDIX 1.4 cont. FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1983

		B R A N C H 2 % of Leaves with Aphids of Number:						
Date	0	1	2	3	4	5	6	>6
April 20	99.5	0.5	0	0	0	0	0	0
27	99	1	0	0	0	0	0	0
May 4	99	1	0	0	0	0	0	0
11	99	1	0	0	0	0	0	0
18	99.5	0.5	0	0	0	0	0	0
25	99.5	0.25	0	0	0.25	0	0	0
June 8	99	0.5	0	0.25	0	0.25	0	0
15	90	5	2	1	1	1	0	0
22	81	8	3	2	2	2	1	1
29	80	7	4	3	2	1	1	2
July 5	81	9.5	4	2	0.5	0.5	0.5	2
13	52	20	10	8	6	2	1	1
20	76	14	4	6	4	3	1	2
27	87	9	3	0.5	0	0	0.5	0
Aug 3	83	12	3	1	0.5	0	0	0.5
10	92	7	0.5	0.25	0	0.25	0	0
17	94	5	1	0	0	0	0	0
24	96	3.75	0	0.25	0	0	0	0
31	96	3	0	1	0	0	0	0
Sept 7	95	3	1	1	0	0	0	0
14	97	2	1	0	0	0	0	0
21	98	1	1	0	0	0	0	0
28	98	1	1	0	0	0	0	0
Oct 5	95	4	1	0	0	0	0	0
12	95	4	1	0	0	0	0	0
19	96	3	1	0	0	0	0	0
26	99	1	0	0	0	0	0	0
Nov 2	99	1	0	0	0	0	0	0
9	99.5	0.5	0	0	0	0	0	0
16	99.5	0.5	0	0	0	0	0	0

APPENDIX 1.5 FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1983

B R A N C H 3

% of Leaves with Aphids of Number:

Date		0	1	2	3	4	5	6	>6
April	20	99.5	0.5	0	0	0	0	0	0
	27	99	1	0	0	0	0	0	0
May	4	99	1	0	0	0	0	0	0
	11	99.5	0.5	0	0	0	0	0	0
	18	99.5	0.5	0	0	0	0	0	0
	25	99.5	0.5	0	0	0	0	0	0
June	8	98.5	0.75	0	0.5	0	0	0	0.25
	15	97	1	0.25	0.5	0	0.5	0.25	0.5
	22	90	4	1	1	1	1	1	1
	29	84	6	3	2	1	1	1	2
July	5	68	14	7	4	1	1	1	4
	13	64	15	7	4	1	1	2	6
	20	64	15	6	5	3	2	1	4
	27	62	22	7	3	2	2	0	2
Aug	3	78	13	4	2	1	0.5	1	0.5
	10	85	9	4	1.5	0	0.5	0	0
	17	90	6	2	1	0.5	0	0	0.5
	24	89	7	2	0.75	0.3	0.3	0.25	0.3
	31	93	5	1.25	0.5	0	0	0	0.25
Sept	7	94	4	1	0.5	0.5	0	0	0
	14	96	3	1	0	0	0	0	0
	21	97	1	1.5	0.5	0	0	0	0
	28	97	2	1	0	0	0	0	0
Oct	5	95	3	1.5	0	0	0.5	0	0
	12	93	5	1.5	0.5	0	0	0	0
	19	96	2	1.5	0.5	0	0	0	0
	26	98	1	1	0	0	0	0	0
Nov	2	98	1	1	0	0	0	0	0
	9	99.5	0.5	0	0	0	0	0	0
	16	99.5	0.5	0	0	0	0	0	0

APPENDIX 1.5 cont. FREQUENCY DISTRIBUTION OF APHIDS - LYNE 1983

		B R A N C H 4 % of Leaves with Aphids of Number:							
Date		0	1	2	3	4	5	6	>6
April	20	0	0	0	0	0	0	0	0
	27	0	0	0	0	0	0	0	0
May	4	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0
	18	0	0	0	0	0	0	0	0
	25	99.75	0	0.25	0	0	0	0	0
June	8	98	1	0.5	0	0.25	0	0	0.25
	15	94	3	2	0.5	0.5	0	0	0
	22	87	5	3	1	1	1	1	1
	29	81.25	8	5	1	1	0.25	0.5	3
July	5	68	15	6	5	2	1	0.5	0.25
	13	71	11	6	4	3	1	1	3
	20	65	15	7	3	2	2	1	5
	27	71	12	8	4	2	1	1	1
Aug	3	80	11	6	1	1	0	0	1
	10	89	8	1	1	0.5	0	0.5	0
	17	92	7	0.5	0.25	0	0.25	0	0
	24	90	6	3	0.25	0.75	0	0	0
	31	96	3	0.75	0	0	0	0	0.25
Sept	7	96	1	2	1	0	0	0	0
	14	96	2	2	0	0	0	0	0
	21	97	2	1	0	0	0	0	0
	28	99	1	0	0	0	0	0	0
Oct	5	99.5	0.5	0	0	0	0	0	0
	12	99.5	0.5	0	0	0	0	0	0
	19	99.5	0.5	0	0	0	0	0	0
	26	99.5	0.5	0	0	0	0	0	0
Nov	2	99.5	0.5	0	0	0	0	0	0
	9	99.5	0.5	0	0	0	0	0	0
	16	99.5	0.5	0	0	0	0	0	0

APPENDIX 1.6 FREQUENCY DISTRIBUTION OF APHIDS - LYNE, 1983

		T H E B U S H % of Leaves with Aphids of Number:						
Date	0	1	2	3	4	5	6	>6
April 20	99.75	0.25	0	0	0	0	0	0
27	99.75	0.25	0	0	0	0	0	0
May 4	99.7	0.3	0	0	0	0	0	0
11	99.75	0.25	0	0	0	0	0	0
18	99.75	0.25	0	0	0	0	0	0
25	99.75	0.125	0	0	0	0.125	0	0
June 8	99.3	0.3	0.13	0.06	0.06	0	0	0.06
15	99	0.5	0.06	0	0.13	0	0.06	0.25
22	90	6	1	1	1	0.5	0.5	1
29	84	8	2	2	1	0.75	0.25	2
July 5	75	10	4	3	1	2	2	3
13	67	12	5	4	2	3	3	4
20	78	11	5	2	1	1	1	1
27	93	5	1	0.5	0.25	0	0	0.25
Aug 3	96	3	0.5	0.25	0.125	0	0	0.125
10	98	1.5	0	0.5	0	0	0	0
17	99	0.5	0.25	0.25	0	0	0	0
24	99	0.5	0.25	0.25	0	0	0	0
31	99	0.75	0.125	0.125	0	0	0	0
Sept 7	99	0.75	0.25	0	0	0	0	0
14	99	0.125	0.125	0.75	0	0	0	0
21	98	1.5	0.5	0	0	0	0	0
28	98	1	1	0	0	0	0	0
Oct 5	99	0.5	0.5	0	0	0	0	0
12	99	1	0	0	0	0	0	0
19	99	1	0	0	0	0	0	0
26	99	1	0	0	0	0	0	0
Nov 2	99.5	0.5	0	0	0	0	0	0
9	99.5	0.5	0	0	0	0	0	0
16	99.5	0.5	0	0	0	0	0	0

AGE STRUCTURE OF THE POPULATION - LF 125 1982

Appendix 2.1

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
29/4	100.0	0	0	0	0	100.0	0	0	0	0					
6/5	0	100.0	0	0	0	0	100.0	0	0	0					
13/5	36.4	27.3	36.4	0	0	21.4	14.3	64.3	0	0					
20/5	90.9	0	9.1	0	0	94.0	0	6.0	0	0					
27/5	58.3	0	6.7	35.0	0	58.0	0	13.3	28.7	0					
3/6	65.6	0	3.1	21.9	9.4	76.7	0	8.3	11.7	3.3					
10/6	100.0	0	0	0	0	36.4	0	9.1	36.4	18.1				-*	
17/6	100.0	0	0	0	0	81.8	0	0	0	18.2	*				
24/6	60.0	0	0	0	40.0	40.0	0	0	0	60.0					
1/7	40.0	20.0	0	0	40.0	52.4	9.5	0	0	38.1					
8/7	62.5	25.0	0	0	12.5	58.3	16.7	0	0	25.0					
15/7	33.3	0	0	0	66.7	83.3	0	0	0	16.7					
22/7	0	0	0	0	0	0	0	0	0	0					
29/7	60.0	0	0	0	40.0	50.0	0	0	0	50.0					
5/8	62.5	0	0	0	37.5	66.7	0	0	0	33.3					
12/8	0	0	0	0	0	0	0	0	0	100.0					-*
19/8	0	0	0	0	0	50.0	0	0	0	50.0	-*				-*
26/8	0	0	0	0	0	0	0	0	0	0					
2/9	0	0	0	0	0	66.7	0	0	0	33.3	-*				-*
9/9	75.0	0	0	0	25.0	0	0	0	0	0	*				*
16/9	0	0	0	0	0	75.0	0	0	0	25.0	-*				-*
23/9	0	0	0	0	0	0	50.0	50.0	0	0		-*	-*		
30/9	33.3	66.7	0	0	0	46.7	13.3	0	13.3	13.3					
7/10	40.0	20.0	0	0	0	32.0	36.0	0	4.0	0					
14/10	40.0	20.0	0	0	0	0	42.8	0	14.3	0	*				

Note: Significance levels are: * $p \leq 0.05$
** $p \leq 0.01$
*** $p \leq 0.001$

A negative sign means that the proportion on the non-terminal leaves was greater than on the terminals, and vice-versa.

AGE STRUCTURE OF THE POPULATION - LF 125 SECTION 1 1983

Appendix 2.2

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
25/4	100.0	0	0	0	0	100.0	0	0	0	0					
2/5	100.0	0	0	0	0	100.0	0	0	0	0					
9/5	83.6	16.4	0	0	0	93.9	0	6.1	0	0	*				
16/5	35.5	15.3	49.2	0	0	33.8	16.9	49.3	0	0					
23/5	86.2	0	13.8	0	0	90.4	0.4	9.2	0	0					
30/5	95.9	0	4.1	0	0	91.2	0	8.8	0	0					
6/6	91.2	0.2	1.5	6.7	0.4	92.2	0.5	0.4	2.3	4.6			*	***	-***
13/6	77.1	1.0	3.9	9.8	8.2	81.3	0.2	2.2	6.4	9.9	-*	*	*	**	
20/6	72.9	0.1	2.9	17.6	6.5	69.8	0	1.7	17.2	11.3			*		-***
27/6	66.5	0	1.6	26.9	5.0	63.2	0	2.0	22.8	12.0	*			**	-***
4/7	72.7	0	0.5	22.1	4.7	54.5	0	0.5	29.2	15.8	***			-***	-***
11/7	81.5	0	0.4	14.5	3.6	58.3	0	0.4	18.9	22.4	***			-***	-***
18/7	59.5	0.4	0.4	9.7	30.0	53.0	0.4	0.6	1.7	44.3	**			***	-***
25/7	88.9	0	0	0	11.1	54.4	0	0	0	45.6		*	*	*	-*
1/8	0	0	0	0	0	84.6	0	0	0	15.4					
8/8	0	0	0	0	0	100.0	0	0	0	0	*				
15/8	0	0	0	0	0	33.3	0	0	0	66.7	*				*
22/8	50.0	0	0	0	50.0	33.3	0	0	0	66.7					
29/8	0	0	0	0	0	100.0	0	0	0	0	*				
5/9	0	0	0	0	0	0	0	100.0	0	0			*		
12/9	0	0	0	0	0	0	100.0	0	0	0		*			
19/9	100.0	0	0	0	0	66.7	0	33.3	0	0					
26/9	0	0	0	0	0	100.0	0	0	0	0	*				
3/10	100.0	0	0	0	0	75.0	16.7	8.3	0	0		*	*		
10/10	0	0	0	0	0	61.1	11.1	0	11.1	0	*	*			

AGE STRUCTURE OF THE POPULATION - LF 125 SECTION 1 1984

Appendix 2.3

PER CENT

	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
Date	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
30/4	100.0	0	0	0	0	100.0	0	0	0	0					
7/5	100.0	0	0	0	0	100.0	0	0	0	0					
14/5	42.3	53.8	3.8	0	0	48.0	36.0	16.0	0	0					
21/5	58.8	14.7	26.5	0	0	72.3	9.2	18.5	0	0					
28/5	90.6	0	9.4	0	0	92.8	0	7.2	0	0					
4/6	92.6	0	1.2	6.2	0	96.7	0	3.3	0	0	-*			**	
11/6	88.2	2.0	2.0	7.8	0	73.8	6.6	4.9	14.7	0					
18/6	87.3	0.6	7.8	1.2	3.1	86.9	0.7	6.6	4.1	1.7					
25/6	76.3	0	2.3	16.8	4.6	73.2	0.4	2.8	18.8	4.8					
2/7	79.4	0	0	11.8	8.8	79.6	0	3.3	9.7	7.4					
9/7	77.0	0	0	8.1	14.9	81.7	0	1.8	8.6	7.9					*
16/7	74.0	0	0.3	15.8	9.9	78.2	0	0.8	12.6	8.4					
23/7	60.5	0.3	0.3	35.1	3.8	57.8	0.3	0.4	31.2	10.3					-***
30/7	79.6	0	0	11.4	9.0	59.4	1.4	0.4	12.4	26.4	***				-***
7/8	18.6	3.4	0	13.5	64.5	53.1	1.1	1.1	9.2	35.5	-***				***
13/8	83.3	0	0	0	16.7	52.7	0	1.9	22.7	22.7					
27/8	50.0	0	0	0	50.0	62.5	0	0	0	37.5					
3/9	0	0	0	0	100.0	83.3	0	0	0	16.7					*
10/9	0	0	0	0	0	100.0	0	0	0	0	-*				
17/9	0	0	0	0	0	100.0	0	0	0	0	-*				
24/9	0	0	0	0	0	100.0	0	0	0	0	-*				
1/10	0	0	0	0	0	60.0	20.0	0	20.0	0	-*	-*		-**	
12/10	0	0	0	0	0	85.7	0	7.1	0	0	-*		-*		
18/10	0	0	0	0	0	85.7	14.3	0	0	0	-*	-*			

AGE STRUCTURE OF THE POPULATION - LF 125 SECTION 2 1984

Appendix 2.4

PER CENT

	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
Date	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
30/4	100.0	0	0	0	0	100.0	0	0	0	0					
7/5	100.0	0	0	0	0	100.0	0	0	0	0					
14/5	62.1	27.6	10.3	0	0	53.8	38.5	7.7	0	0					
21/5	28.6	42.8	28.6	0	0	70.3	13.5	16.2	0	0	-*				
28/5	94.1	0	5.9	0	0	92.8	0	7.2	0	0					
4/6	88.9	0	11.1	0	0	93.7	0	3.4	2.9	0					
11/6	81.0	5.1	3.8	10.1	0	64.4	4.5	2.3	27.6	1.2	*			-**	
18/6	87.7	1.5	3.1	4.6	3.1	87.9	0	5.1	3.0	4.0					
25/6	81.9	0	1.8	10.5	5.8	81.9	0	4.0	10.8	3.3					
2/7	70.0	0.8	2.5	11.7	15.0	74.4	0.4	5.4	10.4	9.4					
9/7	76.4	0	0	11.1	12.5	75.4	0	1.5	13.5	9.6					
16/7	78.3	0	0.4	13.7	7.6	75.4	0	0.5	12.6	11.5					-**
23/7	46.3	0	0	45.8	7.9	56.2	0.3	0.5	28.1	14.9	-*			***	-**
30/7	81.6	0	0	12.2	6.2	56.6	1.0	0.3	11.8	30.3	***				-***
7/8	46.0	0	0	12.7	41.3	48.5	0	0	11.0	40.5					
13/8	0	0	0	0	0	15.4	0	0	30.8	53.8	-*			-*	-*
27/8	40.0	0	0	0	60.0	75.0	0	0	0	25.0	-*				*
3/9	100.0	0	0	0	0	72.7	0	0	0	27.3					-*
10/9	100.0	0	0	0	0	100.0	0	0	0	0					
17/9	100.0	0	0	0	0	100.0	0	0	0	0					
24/9	87.5	0	12.5	0	0	90.9	0	0	0	9.1					
1/10	100.0	0	0	0	0	100.0	0	0	0	0					
12/10	100.0	0	0	0	0	78.6	7.1	0	0	0					
18/10	100.0	0	0	0	0	66.7	0	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110 SECTION (1+2) 1982

Appendix 2.5

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
29/4	0	0	0	0	0	0	0	0	0	0					
6/5	100.0	0	0	0	0	0	0	0	0	0	***				
13/5	0	0	0	0	0	0	0	100.0	0	0			-***		
20/5	100.0	0	0	0	0	75.0	0	25.0	0	0					
27/5	100.0	0	0	0	0	90.9	0	9.1	0	0					
3/6	50.0	37.5	0	0	12.5	66.7	13.3	0	0	20.0					
10/6	81.8	18.2	0	0	0	81.2	10.6	4.7	0	3.5					
17/6	45.2	40.5	7.1	0	7.2	70.1	22.7	5.2	0	2.0	-**	***			
24/6	61.6	16.4	9.6	0	12.4	78.1	9.1	5.4	0	7.4	-**	**			
1/7	73.8	5.6	1.2	14.4	5.0	81.1	1.6	0.6	10.0	6.7	-*	**			
8/7	63.4	2.7	3.8	21.7	8.4	67.4	1.2	3.8	16.3	11.2				*	
15/7	74.0	0	0.9	23.1	2.0	76.3	0	1.6	13.4	8.7				***	-***
22/7	66.4	0	0.3	32.5	0.8	67.0	0	0.4	21.4	11.2				***	-***
29/7	91.4	0.2	0.3	7.2	0.9	82.8	0.4	0.9	8.7	7.2	***		-*		-***
5/8	57.4	1.5	3.3	22.8	15.0	63.5	0.7	2.6	10.9	22.3	-**			***	-***
12/8	78.3	1.6	1.9	5.4	12.9	68.8	0.7	2.0	5.1	23.4	***				-***
19/8	53.9	3.8	0	26.9	15.4	74.6	0.6	2.6	3.4	18.8	-*	*		***	
26/8	76.9	0	0	7.7	15.4	64.5	0.8	1.6	7.3	25.8					
2/9	100.0	0	0	0	0	90.9	0	0	0	9.1					
9/9	100.0	0	0	0	0	66.7	0	13.3	0	20.0					
16/9	100.0	0	0	0	0	0	0	0	0	100.0	***				-***
23/9	100.0	0	0	0	0	60.0	0	20.0	20.0	0					
30/9	100.0	0	0	0	0	50.0	8.3	8.3	33.4	0					
7/10	60.0	0	0	0	0	25.0	16.7	8.3	8.3	0					
14/10	0	0	0	0	0	33.4	33.3	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110 SECTION 1 1983

Appendix 2.6

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
28/4	100.0	0	0	0	0	0	0	0	0	0					
5/5	100.0	0	0	0	0	100.0	0	0	0	0					
12/5	100.0	0	0	0	0	100.0	0	0	0	0					
19/5	80.0	0	20.0	0	0	0	0	0	0	0					
26/5	86.4	4.4	9.1	0	0	75.0	25.0	0	0	0					
2/6	68.4	23.7	7.9	0	0	77.3	18.2	4.5	0	0					
9/6	62.3	28.6	6.5	0	2.6	62.1	29.3	6.9	0	1.7					
16/6	76.5	2.9	15.7	0	4.9	88.6	1.4	9.5	0	0.5	-**				**
23/6	91.3	5.8	2.9	0	0	84.5	9.3	6.2	0	0					
30/6	85.1	0	5.5	5.5	3.9	77.1	2.4	6.0	12.5	2.0				-*	
7/7	82.2	0	2.1	10.3	5.4	80.1	0.1	2.3	7.9	9.6					-***
14/7	78.7	0	0.8	15.1	5.4	65.4	0	0.7	19.2	14.7	***			-***	-***
21/7	87.6	0	0	9.9	2.5	79.8	0	0.1	7.0	13.1	***			***	-***
28/7	76.1	0	0	10.9	13.0	71.0	0.1	0.2	5.3	63.5	*				-*
4/8	48.7	0.6	0	2.6	48.1	83.3	0	0	0	16.7	***				-***
11/8	66.7	0	0	0	33.3	50.0	0	0	0	50.0					
18/8	50.0	0	0	0	50.0	100.0	0	0	0	0					
25/8	100.0	0	0	0	0	100.0	0	0	0	0					
1/9	40.0	20.0	0	0	40.0	0	0	0	0	0					
8/9	0	0	0	0	0	0	0	0	0	0					
15/9	0	0	0	0	0	0	0	0	0	0					
22/9	50.0	0	50.0	0	0	0	100.0	0	0	0					
6/10	0	0	0	0	0	0	0	0	0	0					
13/10	0	0	0	0	0	50.0	50.0	0	0	0					
20/10	0	0	0	0	0	0	0	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110 SECTION 2 1983

Appendix 2.7

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
28/4	100.0	0	0	0	0	0	0	0	0	0					
5/5	100.0	0	0	0	0	100.0	0	0	0	0					
12/5	66.7	33.3	0	0	0	100.0	0	0	0	0					
19/5	77.8	0	12.2	0	0	0	0	100.0	0	0					
26/5	74.1	7.4	18.5	0	0	77.8	11.1	11.1	0	0					
2/6	77.4	9.4	13.2	0	0	76.9	12.3	10.8	0	0					
9/6	73.6	13.7	9.8	0	2.9	78.0	7.6	14.4	0	0					
16/6	74.7	7.7	11.0	3.3	3.3	92.6	0	2.7	2.0	2.7	-***	***	**		
23/6	78.9	8.1	7.3	3.3	2.4	84.8	1.2	7.5	6.2	0.3		***			*
30/6	76.9	6.5	8.6	5.8	2.2	77.1	2.8	5.1	11.5	3.5		*		-*	
7/7	79.3	1.3	4.2	12.2	3.0	82.6	0.1	3.8	7.3	6.2	-*	***		***	-**
14/7	78.0	0	1.2	16.1	4.7	69.7	0	0.6	13.8	15.9	***		**	**	-***
21/7	83.1	0	0.1	13.8	3.0	72.8	0	0.2	7.2	19.8	***			***	-***
28/7	81.1	0.2	0	16.8	1.9	72.5	0.4	0	7.1	19.9	***			***	-***
4/8	45.9	2.3	2.3	12.0	37.5	42.9	0.5	0.9	2.2	53.5				***	-***
11/8	100.0	0	0	0	0	66.7	0	0	0	33.3					
18/8	75.0	0	0	0	25.0	57.1	0	0	0	42.9					
25/8	100.0	0	0	0	0	33.3	0	0	0	66.7					
1/9	0	0	0	0	0	45.5	0	0	0	54.5					
8/9	0	0	100.0	0	0	33.3	0	0	0	66.7					
15/9	0	0	100.0	0	0	0	0	0	0	100.0					
22/9	0	0	0	0	0	66.7	33.3	0	0	0					
29/9	0	0	0	0	0	66.7	0	33.3	0	0					
6/10	0	0	0	0	0	83.3	0	0	0	0					
13/10	0	0	0	0	0	0	8.3	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110 SECTION 3 1983

Appendix 2.8

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
28/4	100.0	0	0	0	0	100.0	0	0	0	0					
5/5	100.0	0	0	0	0	71.4	28.6	0	0	0					
12/5	80.0	20.0	0	0	0	0	0	0	0	0					
19/5	40.0	10.0	50.0	0	0	40.0	0	60.0	0	0					
26/5	88.9	0	11.1	0	0	94.9	0	5.1	0	0					
2/6	86.5	0	13.5	0	0	88.6	4.5	6.8	0	0					
9/6	68.6	17.1	12.9	0	1.4	75.0	15.6	6.3	0	3.1					
16/6	82.2	3.4	8.5	1.7	4.2	82.7	3.8	11.3	0.8	1.4					
23/6	83.0	1.9	5.0	8.9	1.2	87.0	1.6	5.7	5.3	0.4					
30/6	71.0	0.9	4.2	20.3	3.6	75.6	0.6	3.1	14.1	6.6					-*
7/7	84.9	0.1	2.4	8.9	3.7	82.8	0.2	1.7	7.6	7.7					-***
14/7	71.7	0	0.5	17.7	10.1	50.5	0	0.4	16.0	33.1	***				-***
21/7	72.7	0	0	19.1	8.2	65.7	0	0	4.3	30.0	***			***	-***
28/7	55.8	0	0	1.6	42.6	56.4	0.4	0	2.8	40.4			***		
4/8	18.2	0	0	0	81.8	46.5	0	0	0	53.5					
11/8	0	0	0	0	0	0	0	0	0	0					
18/8	66.7	0	0	0	33.3	33.3	0	0	0	66.7					
25/8	0	0	0	0	0	100.0	0	0	0	0					
1/9	0	0	0	0	100.0	0	0	0	0	100.0					
8/9	0	0	0	0	0	0	0	0	0	0					
15/9	0	0	0	0	0	0	0	0	0	0					
22/9	0	0	0	0	0	0	0	0	0	0					
29/9	0	0	0	0	0	0	0	0	0	0					
6/10	0	0	0	0	0	0	0	0	0	0					
13/10	0	0	0	0	0	0	0	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110 SECTION 1 1984

Appendix 2.9

PER CENT

	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES		
26/4	0	0	0	0	0	0	0	0	0	0			
3/5	0	0	0	0	0	0	0	0	0	0			
10/5	0	0	0	0	0	0	0	0	0	0			
17/5	0	0	0	0	0	0	0	0	0	0			
24/5	0	0	0	0	0	0	0	0	0	0			
31/5	0	0	0	0	0	0	0	0	0	0			
7/6	0	0	0	0	0	100.0	0	0	0	0			
14/6	0	0	0	0	0	100.0	0	0	0	0			
21/6	0	0	0	0	0	100.0	0	0	0	0			
28/6	100.0	0	0	0	0	75.0	0	16.7	0	8.3			
5/7	75.0	50.0	5.0	7.5	7.5	83.8	1.7	9.4	0	5.1			**
12/7	85.3	0	3.2	4.2	7.3	84.2	0	2.8	5.1	7.9			
19/7	77.7	0	5.8	14.1	2.4	79.6	0	4.1	9.9	6.4			-*
26/7	76.6	0	0.8	17.5	5.1	73.9	0.1	0.4	15.7	9.9			-***
2/8	80.0	0.4	0	10.5	9.1	68.8	0.2	0.2	7.0	23.8	***	***	-***
9/8	85.8	0.4	0.6	10.1	3.1	83.1	0.4	0,3	6.8	9.4		**	-***
16/8	71.5	6.2	0.2	13.4	8.7	61.4	5.2	0.9	12.1	20.4	***		-***
27/8	60.2	2.2	1.6	15.6	20.4	57.2	1.3	3.1	11.2	27.2			
30/8	60.1	1.3	2.5	3.8	32.3	58.7	0.4	1.8	3.2	35.9			
6/9	88.9	0	0	0	11.1	87.3	3.6	0	0	9.1			
13/9	87.5	0	0	0	12.5	79.2	0	0	4.2	16.6			
20/9	85.7	0	0	14.3	0	78.6	0	7.1	14.3	0			
27/9	50.0	0	0	50.0	0	73.3	0	13.3	0	13.4			
5/10	100.0	0	0	0	0	61.5	7.7	7.7	15.4	0			
12/10	100.0	0	0	0	0	86.7	6.7	0	0	0			

AGE STRUCTURE OF THE POPULATION - WM 110 SECTION 2 1984

Appendix 2.10

PER CENT

	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
Date	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
26/4	0	0	0	0	0	0	0	0	0	0					
3/5	0	0	0	0	0	0	0	0	0	0					
10/5	0	0	0	0	0	0	0	0	0	0					
17/5	0	0	0	0	0	0	0	0	0	0					
24/5	0	0	0	0	0	0	0	0	0	0					
31/5	0	0	0	0	0	100.0	0	0	0	0					
7/6	0	0	0	0	0	100.0	0	0	0	0					
14/6	100.0	0	0	0	0	100.0	0	0	0	0					
21/6	100.0	0	0	0	0	33.3	66.7	0	0	0					
28/6	89.3	7.1	3.6	0	0	79.2	8.3	12.5	0	0					
5/7	62.2	5.4	9.5	12.1	10.8	65.7	4.5	15.7	8.2	5.9					
12/7	86.8	0	1.9	1.9	9.4	85.2	0.2	2.9	6.9	4.8			-*	*	
19/7	84.0	0	1.0	14.0	1.0	79.6	0	0.9	14.6	4.9	**			-***	
26/7	61.9	0	0.9	31.9	5.3	73.1	0	0.8	17.6	8.5	-***		***	-***	
2/8	74.2	0	0.1	19.4	6.3	70.5	0	0.3	10.1	19.1	**		***	-***	
9/8	78.4	0	0.4	18.8	2.4	73.3	0.8	0.5	11.4	14.0	***	-**	***	-***	
16/8	75.4	4.0	2.4	12.0	6.2	65.8	3.3	2.4	13.0	15.5	***			-***	
27/8	79.0	1.0	1.0	8.6	10.4	56.8	2.1	4.8	8.2	28.1	***			-***	
30/8	63.6	0	0	4.6	31.8	63.2	0.5	0.5	2.9	32.9					
6/9	60.0	0	0	0	40.0	86.3	0	1.4	2.7	9.6				*	
13/9	0	0	0	0	0	61.9	0	0	0	33.3	-*			-*	
20/9	100.0	0	0	0	0	82.7	4.3	13.0	0	0					
27/9	100.0	0	0	0	0	80.0	0	10.0	0	0					
5/10	0	0	0	0	0	50.0	50.0	0	0	0					
12/10	0	0	0	0	0	0	0	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110 SECTION 3 1984

Appendix 2.11

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
26/4	0	0	0	0	0	0	0	0	0	0					
3/5	0	0	0	0	0	0	0	0	0	0					
10/5	0	0	0	0	0	0	0	0	0	0					
17/5	0	0	0	0	0	0	0	0	0	0					
24/5	0	0	0	0	0	0	0	0	0	0					
31/5	0	0	0	0	0	0	0	0	0	0					
7/6	0	0	0	0	0	0	0	0	0	0					
14/6	0	0	0	0	0	0	0	0	0	0					
21/6	0	0	0	0	0	0	0	0	0	0					
28/6	50.0	33.3	16.7	0	0	75.0	8.3	16.7	0	0					
5/7	68.6	11.4	8.6	0	11.4	73.5	5.9	14.0	1.5	5.1					
12/7	88.7	0	4.5	2.3	4.5	87.3	0.6	2.3	2.3	7.5					
19/7	83.1	0	0.8	13.7	2.4	82.4	0	0.7	12.8	4.1					
26/7	84.9	0	0.9	10.9	3.3	76.5	0	0.3	13.0	10.2	***				-***
2/8	82.8	0	0.6	6.9	9.7	71.6	0	0.5	8.0	19.9	***				-***
9/8	79.5	1.4	0.5	11.2	7.4	77.8	1.4	0	4.7	16.1				***	-***
16/8	78.1	3.6	1.5	8.7	8.1	65.3	2.9	1.6	10.6	19.6	***				-***
27/8	56.9	0	6.2	7.7	29.2	57.0	0	1.9	5.8	35.3					
30/8	58.8	1.2	1.2	0	38.8	61.5	0	0.2	0.6	37.7					
6/9	100.0	0	0	0	0	83.3	0	0	0	16.7					
13/9	0	0	0	0	0	83.3	0	0	0	16.7					
20/9	0	0	0	0	0	100.0	0	0	0	0					
27/9	0	0	0	0	0	100.0	0	0	0	0					
5/10	0	0	0	0	0	0	0	0	0	0					
12/10	0	0	0	0	0	0	0	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110, 3.5 m 1983

Appendix 2.12

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
28/4	0	0	0	0	0	0	0	0	0	0					
5/5	0	0	0	0	0	0	0	0	0	0					
12/5	100.0	0	0	0	0	0	0	0	0	0					
19/5	0	0	100.0	0	0	0	0	0	0	0					
26/5	50.0	0	50.0	0	0	100.0	0	0	0	0					
2/6	88.0	5.0	7.0	0	0	75.0	8.3	16.7	0	0					
9/6	83.0	7.0	9.0	1.0	0	84.2	0	15.8	0	0					
16/6	87.0	4.0	4.0	3.0	2.0	94.0	0	3.4	2.6	0					
23/6	79.0	7.0	7.0	5.0	2.0	85.2	1.4	5.1	5.9	2.4		*			
30/6	78.5	5.5	6.6	6.9	2.5	86.4	0.3	2.1	7.9	3.3	-*	***	**		
7/7	79.5	2.1	3.9	11.1	3.4	84.5	0.1	1.9	6.4	7.1		***	*	**	-**
14/7	78.5	0	1.1	14.9	5.5	73.2	0	0.1	11.9	14.8	***		***	***	-***
21/7	84.6	0	0.2	12.9	2.3	74.8	0	0	6.8	18.4	***		***	***	-***
28/7	83.4	0.1	0	15.1	1.4	73.4	0.1	0	6.7	19.8	***			***	-***
4/8	47.6	2.1	3.1	10.8	36.4	47.9	0.3	0.6	2.1	49.1			*	***	-*
11/8	75.0	0	0	0	25.0	63.6	0	0	0	36.4					
18/8	75.1	0	0	0	25.0	50.0	0	0	0	50.0					
25/8	100.0	0	0	0	0	75.0	0	0	0	25.0					
1/9	100.0	0	0	0	0	80.0	0	0	0	20.0					
8/9	0	0	0	0	0	0	0	0	0	0					
15/9	0	0	100.0	0	0	100.0	0	0	0	0					
22/9	0	0	100.0	0	0	100.0	0	0	0	0					
29/9	50.0	0	50.0	0	0	50.0	50.0	0	0	0					
6/10	0	0	0	0	0	0	100.0	0	0	0					
13/10	0	0	0	0	0	0	0	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110, 7.5 m 1983

Appendix 2.13

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
28/4	0	0	0	0	0	0	0	0	0	0					
5/5	0	0	0	0	0	0	0	0	0	0					
12/5	0	0	0	0	0	0	0	0	0	0					
19/5	0	0	0	0	0	100.0	0	0	0	0					
26/5	100.0	0	0	0	0	66.6	0	33.3	0	0					
2/6	75.3	7.4	17.3	0	0	67.8	11.1	21.1	0	0					
9/6	76.1	14.3	9.6	0	0	77.9	9.1	13.0	0	0					
16/6	75.8	6.9	14.1	1.1	2.1	91.4	2.1	3.1	2.3	1.1	-*		*		
23/6	80.6	7.0	6.1	3.2	3.1	87.9	1.1	5.9	4.1	1.0		**			
30/6	81.5	3.1	7.0	5.6	2.8	83.9	2.8	4.1	5.1	4.1					
7/7	81.5	1.4	3.0	11.1	3.0	85.6	0.4	1.1	6.0	6.9	-*	*	**	***	-***
14/7	76.2	0	0.4	18.3	5.1	76.0	0	0.1	11.1	12.8				***	-***
21/7	81.4	0	0.1	14.1	4.4	75.8	0	0	6.1	18.1	***			***	-***
28/7	79.8	0	0	12.1	8.1	73.8	0.1	0	6.8	19.3	*			***	-***
4/8	68.8	0.2	0	11.1	19.9	69.6	0.8	0.4	3.1	26.1				***	-**
11/8	0	0	0	0	0	75.0	0	0	0	25.0					
18/8	0	0	0	100.0	0	66.7	0	0	0	33.3					
25/8	0	0	0	0	0	100.0	0	0	0	0					
1/9	0	0	0	0	0	0	0	100.0	0	0					
8/9	0	0	0	0	0	100.0	0	0	0	0					
15/9	100.0	0	0	0	0	100.0	0	0	0	0					
22/9	0	0	0	0	0	0	0	0	0	0					
29/9	0	0	0	0	0	0	0	0	0	0					
6/10	0	0	0	0	0	100.0	0	0	0	0					
13/10	0	0	0	0	0	0	0	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110, 3.5 m 1984

Appendix 2.14

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
26/4	0	0	0	0	0	0	0	0	0	0					
3/5	0	0	0	0	0	0	0	0	0	0					
10/5	0	0	0	0	0	0	0	0	0	0					
17/5	0	0	0	0	0	0	0	0	0	0					
24/5	0	0	0	0	0	0	0	0	0	0					
31/5	0	0	0	0	0	25.0	25.0	50.0	0	0					
7/6	100.0	0	0	0	0	0	0	0	0	0					
14/6	0	66.7	33.3	0	0	75.0	0	25.0	0	0					
21/6	16.7	50.0	33.3	0	0	100.0	0	0	0	0					
28/6	44.5	22.2	33.3	0	0	60.0	20.0	20.0	0	0					
5/7	80.0	16.0	0	0	4.0	76.0	1.1	17.1	2.9	2.9		***	-***		
12/7	88.5	0	0	0	11.5	82.5	0.3	3.5	4.5	9.2					
19/7	86.6	0	3.0	8.4	2.0	85.0	0	1.5	7.5	6.0			*		-***
26/7	70.4	0	0.2	20.0	9.4	72.1	0	0.8	16.2	10.9			-*	**	
2/8	85.5	0	0	12.8	1.7	72.1	0	0.5	11.3	16.1	***		-*		-***
9/8	77.6	0	0.6	16.2	5.6	74.4	0.2	0.2	11.3	13.9				***	-***
16/8	70.4	0.7	0	12.1	16.8	54.9	3.9	1.2	11.3	28.7	***	-**	-*		-***
27/8	67.8	0	0	0	32.2	64.3	0.5	0.7	1.2	33.3					
30/8	52.6	0	0	0	47.4	58.1	0	3.8	0	38.1					
6/9	80.0	0	0	0	20.0	80.0	0	8.0	0	12.0					
13/9	87.5	0	0	0	12.5	100.0	0	0	0	0					
20/9	100.0	0	0	0	0	100.0	0	0	0	0					
27/9	81.8	9.1	9.1	0	0	33.3	0	33.3	0	0					
5/10	66.7	22.2	11.1	0	0	0	50.0	0	0	0					
12/10	14.3	42.8	0	0	0	0	0	0	0	0					

AGE STRUCTURE OF THE POPULATION - WM 110, 7.5m 1984

Appendix 2.15

PER CENT

Date	TERMINAL LEAVES					NON-TERMINAL LEAVES					SIGNIFICANT DIFFERENCES IN AGE STRUCTURES				
	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults	Nymphs	IV Apterae	Apterous Adults	IV Alatae	Alatae Adults
26/4	0	0	0	0	0	0	0	0	0	0					
3/5	0	0	0	0	0	0	0	0	0	0					
10/5	0	0	0	0	0	0	0	0	0	0					
17/5	0	0	0	0	0	0	0	0	0	0					
24/5	0	0	0	0	0	0	0	0	0	0					
31/5	0	0	0	0	0	100.0	0	0	0	0					
7/6	0	0	0	0	0	100.0	0	0	0	0					
14/6	0	0	0	0	0	50.0	50.0	0	0	0					
21/6	100.0	0	0	0	0	57.1	0	28.6	0	14.3					
28/6	50.0	50.0	0	0	0	50.0	0	25.0	0	25.0					
5/7	73.7	0	10.5	5.3	10.5	93.5	0	3.7	0	2.8					
12/7	86.7	0	3.3	0	10.0	92.1	0	1.5	0.5	5.9			*		
19/7	91.9	0	0	2.7	5.4	87.2	0	0.1	2.6	10.1					
26/7	77.1	0	0	7.6	15.3	77.4	0	0.1	5.1	17.4					
2/8	67.9	0	0	13.8	18.3	76.9	0	0	5.1	18.0	-***		***		
9/8	63.3	1.7	0	31.7	3.3	68.4	0	0	19.1	12.5		*		**	-**
16/8	70.6	0	2.7	8.0	18.7	60.9	0.6	0	5.6	32.9	*		**		-***
27/8	80.6	0	8.3	2.8	8.3	61.2	0.9	0.9	0.9	36.1	***		***		-***
30/8	50.0	0	0	0	50.0	71.7	2.7	2.7	0	22.9					
6/9	100.0	0	0	0	0	82.7	0	4.3	0	13.0					
13/9	0	100.0	0	0	0	100.0	0	0	0	0					
20/9	0	0	0	0	0	100.0	0	0	0	0					
27/9	50.0	0	50.0	0	0	100.0	0	0	0	0					
5/10	100.0	0	0	0	0	33.3	33.3	33.3	0	0					
12/10	0	0	0	0	0	33.3	33.3	16.7	0	0					